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The Mazon Creek Caridoid Crustacea

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INTRODUCTION

The importance of the Middle Pennsylvanian Mazon Creek Essex fauna Crustacea was established with the conclusions drawn from the study of the Hoplocarida (Schram, 1969a, b, c). In this present paper shrimp which have been referred to the superorder Eocarida are examined. These shrimp are from both the Essex and Braidwood faunas (Johnson and Richardson, 1966).

The Eocarida contain the most extensive of the Late Paleozoic groups of Eumalocastraca. These crustaceans are found all over the world, from the Middle Devonian to the Late Permian (Schram, 1969a). The superorder Eocarida was erected by Brooks (1962). Brooks took a number of Paleozoic forms, which had been moved about from one higher taxonomic category to another, and placed them together within a single group. These forms were all characterized by Brooks as having well-developed caudal spines and lobes, the protopod of the thoracic appendages as a single element ("sympod"), and the presence of oostegites and/or seminal receptacles variously developed.

The Eocarida exhibit marked similarities to many of the modern forms and indeed were originally classified into various living groups. The pygocephalomorphs were, previous to Brooks work, frequently referred to as "macrurous decapods." The eocaridaceans were often placed in either the Mysidacea or Euphausiacea. Consequently, it has been suggested that perhaps the roots of the modern radiation are to be found in the Eocarida. This question shall be examined in this paper.

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PLATE 1. *Belotelson magister*, counterpart of PE 16371 in the collection of Mrs. Trudy Becker, X 1.8.

New morphologic data has come to light to cast doubt on the separation of the eocarid groups into a separate superorder. The pygocephalomorphs now appear to be a specialized form of mysidacean peracarid. The eocaridaceans are possibly referable to several different schizopod groups but are left as eocarids for the time being.

Specimens from a number of public and private collections have been used in this study. Prefixes denote the collections in which these specimens may be found.

PE—Field Museum of Natural History
USNM—United States National Museum
YPM—Peabody Museum, Yale University
D—Private collection of Mr. Kenneth Davenport, formerly of Chicago, Illinois
G—Private collection of the Calvin George family, Naperville, Illinois
H—Private collection of Mr. Jerry Herdina, Berwyn, Illinois
K—Private collections of Mr. and Mrs. James Koneckny, Prescott, Arizona
HTP—Private Collection of Mr. and Mrs. Ted Pieko, Chicago, Illinois

SYSTEMATICS

Superorder PERACARIDA Calman 1904
Order MYSIDACEA Boas 1883
Suborder PYGOCEPHALOMORPHA Beurlen 1930

Carapace with branchiostegal development; abdomen equal in length to the thorax or reduced; females with oöstegites and seminal receptacle; well-developed caudal spines and furcae.

Occurrence.—Lower Mississippian - Upper Permian.

Family PYGOCEPHALIDAE, Brooks 1962

Carapace with antero-lateral spines.

Occurrence.—Lower Pennsylvanian-Lower Permian.

Mamayocaris, Brooks 1962

Short antero-lateral spines followed typically by five branchiostegal serrations; posteriorly directed cervical groove; telson subtriangular; females with seminal receptacles (oostegites not observed).

Occurrence.—Middle Pennsylvanian-Lower Permian.

Mamayocaris jaskoskii, new species

Diagnosis.—Moderate in size; small caudal furcae; accessory projection of telson over the caudal spine; sigmoid diaresis on exopod of the uropod.

Description.—The carapace is smooth except for a posteriorly directed cervical groove and gastric spine. The falciform rostrum (PE 10372, fig. 2, PE 12344) is moderate in length as are the anterolateral spines (H 290, fig.

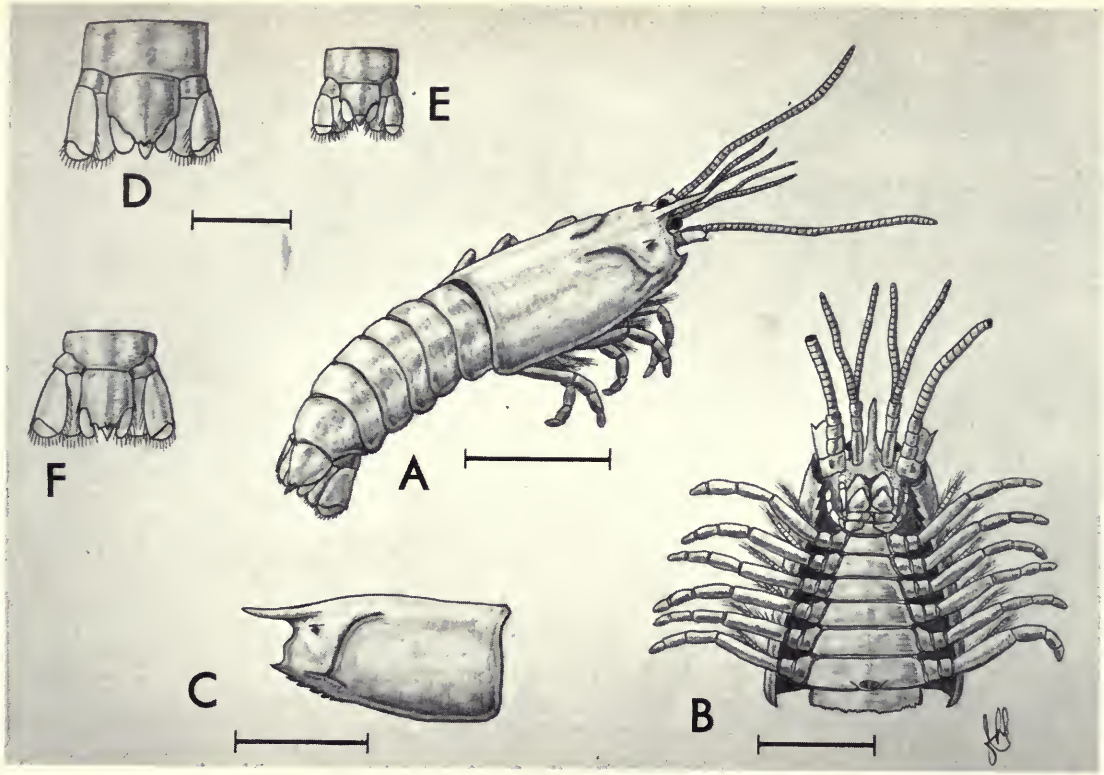

FIG. 1. Scales indicate 1 cm. **A-D**, *Mamayocaris jaskoskii*, reconstructions of various parts of the body. **E**, tail fan of *Mamayocaris jepseni*, redrawn from Brooks, 1962. **F**, tail fan of *Anthracaris gracilis*, redrawn from Brooks, 1962.

FIG. 2. *M. jaskoskii*. Latex mold of PE 10372, arrows indicating falciform rostrum and gastric spines. X 2.6.

3). There are typically five branchiostegal serrations, though there may be an incipient sixth spine (H 290, PE 12991).

The first antenna has three segments in the peduncle with two flagella (PE 11261, PE 16100, HTP 1572). The second antenna is larger than the first, possesses three large basal segments and a large scale-like scaphocerite (PE 21921, HTP 1449). The eyes, like those of *M. jepseni*, are moderately large (PE 11361, fig. 4, HTP 1312).

The mandibles are obscured by the overlying maxillae and maxillipeds. The maxillae have large gnathobasic coxae and palps with an interminable number of segments (PE 21918, fig. 5; H 290, fig. 6). There were two maxillipeds, each with four or five segments and the coxa as a gnathobase (PE 21906, fig. 7; HTP 1572, fig. 8). The walking legs are of typical pygocephalid form (HTP 82): the protopod consists of two

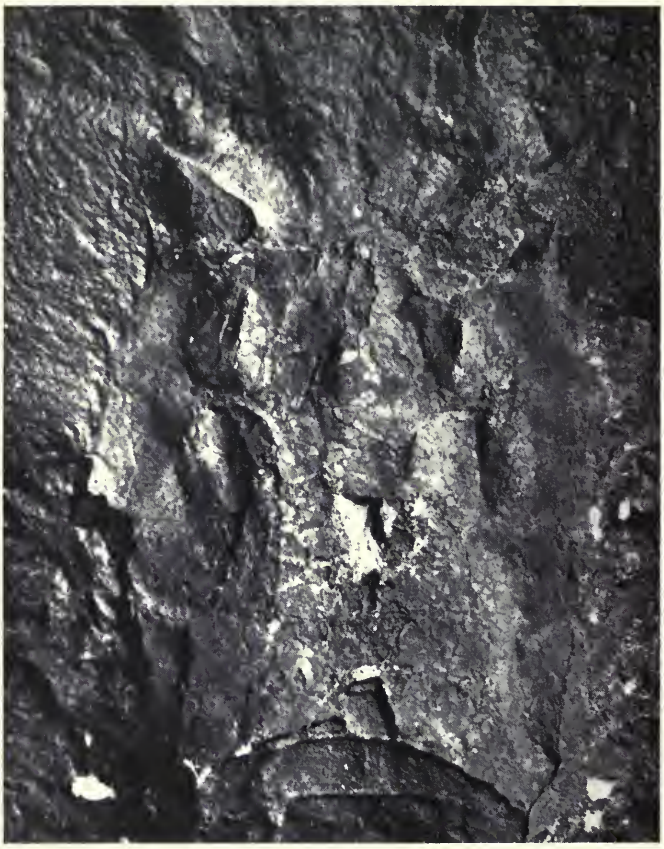

FIG. 3. *M. jaskoskii.* H 290, with anterolateral spines and branchiostegal serrations. X 5.3.

segments (PE 21906, fig. 10), the endopod (H 287, fig. 9) is similar to that of *M. jepseni* and *Anthracaris gracilis* with four segments, and there is an annulate exopod (PE 21906, HTP 1572). The thoracopods articulate on the lateral margins of broad sternites.

Sexes can be readily distinguished. The females have a large seminal receptacle opening on the eighth sternite of the thorax (HTP 1572, fig. 11).

No pleopods have been observed on the abdominal segments. The taxonomically important telson and uropods effectively distinguish *M. jaskoskii* from *M. jepseni*. The telson is subtriangular and is indented along its margins where the caudal lobes articulate. There is a blunt, median accessory projection of the telson extending out over the caudal spine (HTP 11236, fig. 12; HTP 1449). The flap-like endopods and

FIG. 4. *M. jaskoskii.* PE 11361, holotype, both counterparts.

exopods of the uropods bear a fringe of setae along their posterior margins as does the exopod about the diaresis (HTP 11236, fig. 13). The course of the exopodal diaresis shifts posteriad as it proceeds medially, forming an "S"-shaped path.

A reconstruction of this animal is offered in Figure 1.

Remarks.—Mamayocaris jaskoskii occurs in moderate numbers in the Essex fauna. It does not occur at all in the Braidwood facies. It is larger than the Braidwood pygocephalomorph, *Anthracaris gracilis* (Meek and Worthen) 1865, and considerably larger than the Permian *Mamayocaris jepseni* Brooks, 1962. Statistical data for these three species are offered in Table 1. The high value of "V" seems to be due to sampling different age groups, or molt stages. When relatively homogeneous groups were used,

FIG. 5. *M. jaskoskii.* PE 21918, closeup of ventral cephalothorax with gnathobase of second maxilla (mx_2), palps of first maxilliped (mp_1), and coxa (c) and basis (b) of pereiopodal protopods. X 7.2.

TABLE 1. Statistical data for three species of pygocephalids.[1]

Mamayocaris jaskoskii

	N	$\bar{x}$	s	Range	V
Carapace length	51	1.68±.05	.34	1.08-2.35	20.2
Abdomen length	10	1.82±.16	.51	1.10-3.00	28.0
Body (optic notch to telson base)	16	3.57±.13	.51	2.7 -4.57	14.3
Rostrum	4	.54±.12	.23	.35- .75	42.7
Tail fan length	8	.73±.06	.16	.53-1.05	21.9

Mamayocaris jepseni

	N	$\bar{x}$	s	Range	V
Carapace length	20	.74±.02	.08	.56- .85	10.8
Abdomen length	7	.53±.02	.05	.46- .60	9.4

Anthracaris gracilis

	N	$\bar{x}$	s	Range	V
Carapace length	64	1.4 ±.02	.16	.8 -1.8	11.4

[1]*Mamayocaris jaskoskii* based on measurable specimens in the collections of Field Museum, Mr. and Mrs. Ted Piecko, and Mr. Levi Sherman. *Mamayocaris jepseni* based on measurements taken by the author from the paratype material at Princeton University. *Anthracaris gracilis* taken from Brooks (1962).

such as for *M. jepseni*, the value of "V" was lower. If the samples were large enough to enable separation of the various molt stages, the variances would then probably be more normal.

The environmental regimes of the two species of *Mamayocaris* are different. The Middle Pennsylvanian Mazon Creek species occurs in a marine facies of a near shore, deltaic, flood-plain environment. The Permian species, *M. jepseni*, is found in the Vale Formation near Lawn, Texas, and the Opeche Formation west of Rapid City, South Dakota, both lagoonal facies. The only features in common between all three of these localities is that they are shallow, near shore, marine environments in which there were probably incursions of fresh water of varying degrees.

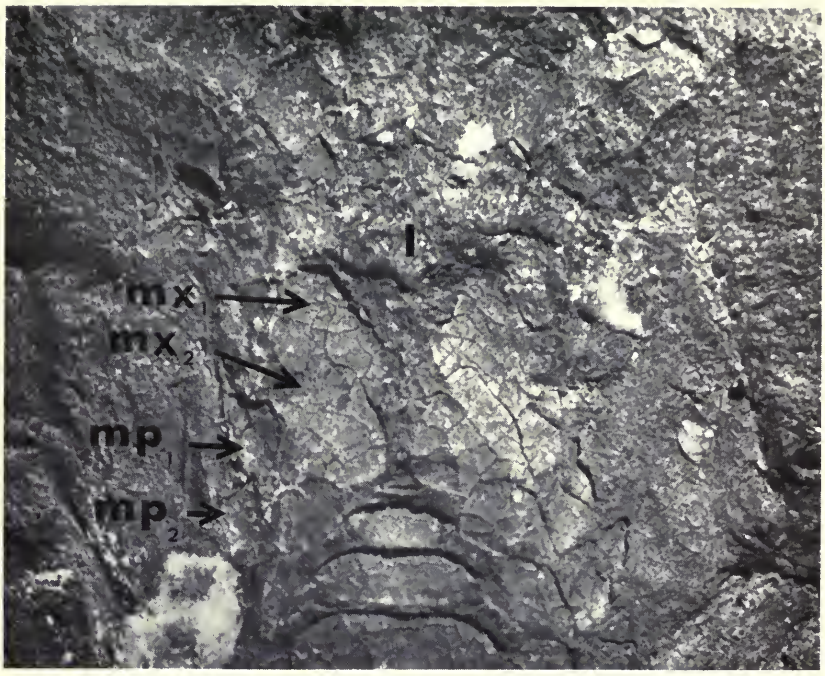

FIG. 6. *M. jaskoskii.* H 290, closeup of ventral cephalon with labrum (1), maxillae (mx_1 and mx_2), and palps of maxillipeds (mp_1 and mp_2). X 5.5.

It is interesting to note that, although readily distinguishable from *Anthracaris gracilis*, *Mamayocaris jaskoskii* is almost identical to *M. jepseni*, except for size and variation of the tail fan. In *M. jepseni* the caudal lobes are larger, there is no median accessory projection over the caudal spine, and the uropodal diaresis is straight and not directed posteriad. The details of the tail fan of *M. jaskoskii* are reminiscent of that of *Pygocephalus dubius* as reconstructed by Brooks (1962).

Two exceptional specimens, HTP 11175 and HTP 11642 (figs. 14, 15), from the collection of Mr. and Mrs. Ted Piecko of Chicago, Illinois, give us an insight into the post-larval development of *Mamayocaris jaskoskii*. HTP 11175 has a carapace length of 3.4 mm. and appears to be a post-larval juvenile. Both specimens are considerably smaller than the adult *Mamayocaris* in the sample (mean carapace length of 16.8 mm.). Species identification of these mini-forms might be questioned; but they are pygocephalomorphs collected from the Essex fauna locality, and as far as can be determined from branchiostegal and anterolateral spines, and cephalic grooves they are assignable to *M. jaskoskii* as juvenile individuals.

HTP 11175 has a carapace as broad as it is long. There is only the slightest indication of a rostrum and anterolateral spines. The branchiostegal spines are poorly developed except for the two anterior ones and the fifth spine is hardly developed at all. There is no indication of cephalic grooves. The first antenna has a peduncle of three segments and only one of the flagella is preserved on this specimen. The peduncle of the second antenna is shorter than that of the first and also has three segments, and an oval scaphocerite is present. The flagellum of the second antenna is large, well developed, and in this specimen (as far as preserved) almost as long as the carapace. Some of the thoracic appendages are partly preserved. Little can be deduced concerning them except that it would appear that the protopods of these appendages are possibly located near the midline instead of lateral to a broad sternite, as is the case in the adults. Only the first abdominal segment is visible. The rest of the

FIG. 7. *M. jaskoskii*. PE 21906, closeup of mouthparts with second maxilla (mx_2) with remnants of palp indicated by arrow, and maxillipeds (mp_1 and mp_2). X 10.3.

abdomen appears to be tucked up underneath the thorax. This, of course, could be merely due to contraction of the abdominal flexors at the time of death but the possibility remains that the abdomen might have been

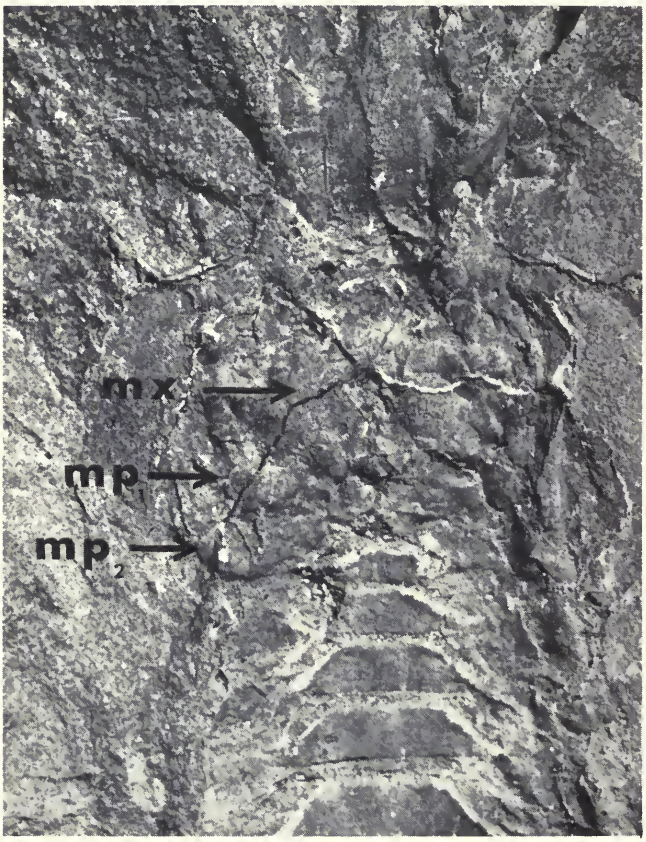

FIG. 8. *M. jaskoskii*. HTP 1572 with second maxilla (mx_2) and the two maxillipeds (mp_1 and mp_2). X 6.

naturally carried under the abdomen at this stage, much as it is in the Permian pygocephalomorphs and the true crabs.

HTP 11642 has a carapace longer than it is wide. Indeed the ratio of length to width is greater than in the adult *M. jaskoskii*, more akin to the condition found in *Pygocephalus dubius*. The rostrum is only moderately developed, the anterolateral spines are present, and only four branchiostegal spines are noted on this specimen. The gastric spines are present along with the cephalic grooves. These grooves, however, are not directed posteriorly as much as they are in the adults. As far as can be

FIG. 9. *M. jaskoskii.* H 287, male showing the distal portions of the thoracopods. X 3.6.

FIG. 10. *M. jaskoskii.* PE 21906, closeup of pereiopods with coxa (c), basis (b), and thoracopodal exopods (ex). X 10.3.

FIG. 11. *M. jaskoskii*. HTP 1572, female with seminal receptacle on the eighth thoracic sternite. X 2.

determined, the antennae resemble those of the adults, except that the scaphocerite is still oval in shape. The thoracic appendages have not been preserved at all. The thoracic sternites are well developed, however, and there is no seminal receptacle opening on the eighth segment. Part of the tail fan is preserved and, from what can be discerned, resembles somewhat that of *Mamayocaris jepseni* as reconstructed by Brooks (1962). The proximal portion of the telson is rectangular while the distal part is subtriangular. The telson is notched on its margin at the junction of these two portions to accommodate the caudal lobes. Little can be said concerning the uropods except that they are present.

Although it would be better to have a whole array of specimens on which to base any statements concerning the ontogeny of *Mamayocaris jaskoskii*

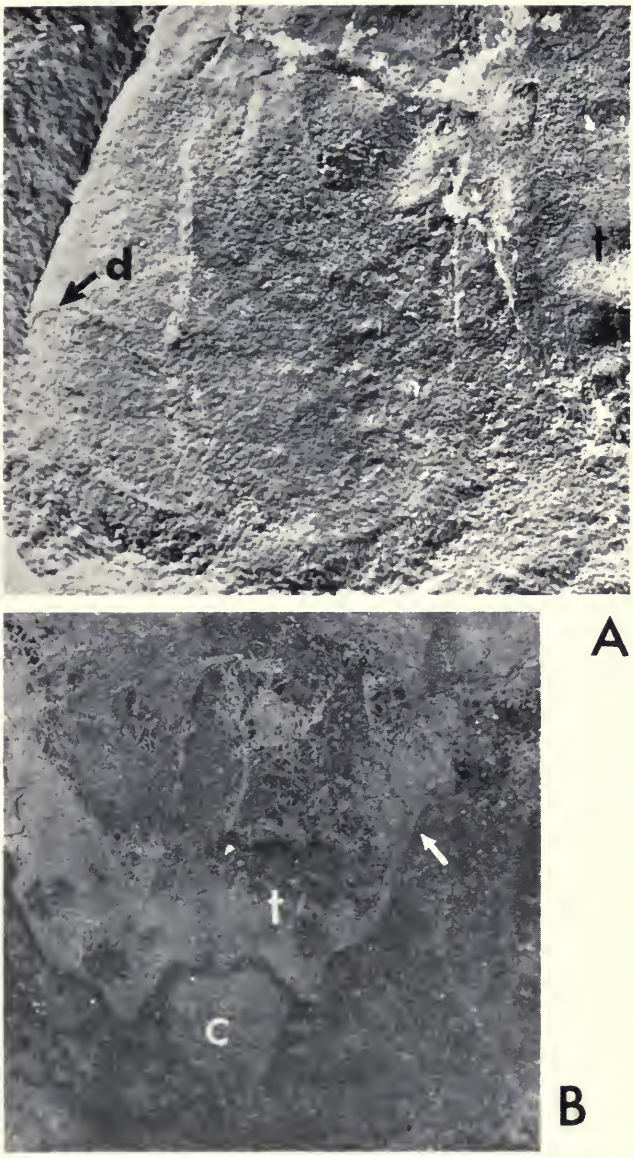

FIG. 12. *M. jaskoskii.* HTP 11236. **A**, under normal lighting showing part of diaresis (d) on uropod and telson (t). **B**, under xylene with telson (t) and caudal spine (c); note indentations for the caudal lobes (arrow). Both X 7.2.

some salient features can be discerned here. Carapace development apparently proceeded from a square to a rectangular shape. There was a gradual development of the rostrum, cephalic grooves, and the spines

FIG. 13. *M. jaskoskii*. HTP 11236. Under low angle lighting with part of gut impression (g) in the telson, caudal spine (c), and setae (s) on uropodal margins. X 7.8.

(gastric, anterolateral, and branchiostegal). It is possible that the bases of the thoracic legs moved from a medial position to their adult lateral position, and that the abdomen may have developed from a primarily flexed position to an extended one. The caudal lobes of the telson moved more mediad and posteriad as the adult condition was approached.

It is interesting to note that the most juvenile of these Pygocephalidae exhibit a primary character of the Permian Notocarididae, i.e., the flexed abdomen. It is tempting to suggest that perhaps the notocarids arose from the pygocephalids by neoteny. Some resemblances can also be seen to other pygocephalid species, viz. the carapace of *Pygocephalus dubius*, and *Mamayocaris jepseni*. As is frequently the case among modern forms, a detailed knowledge of the development of the pygocepholomorphs, both larval and juvenile, would undoubtedly clarify the phylogeny and

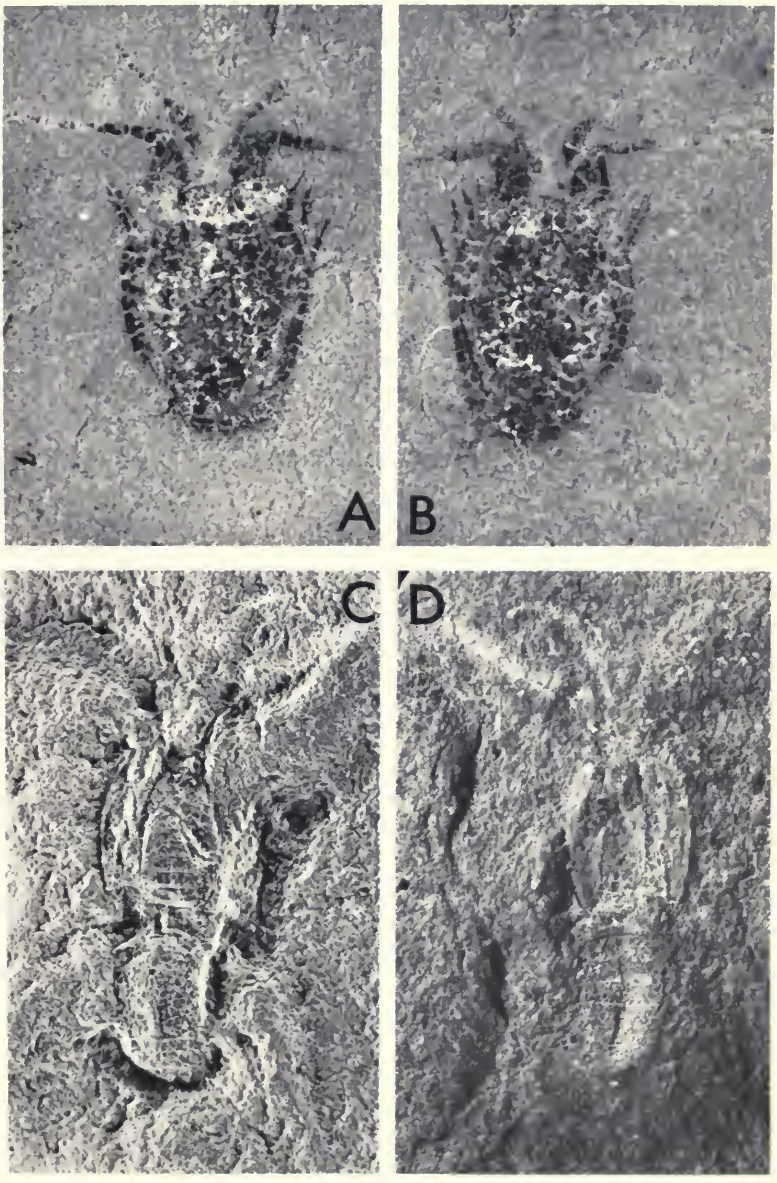

FIG. 14. *M. jaskoskii*. **A**, **B**, HTP 11175 early juvenile stage. X 7.4. **C**, **D**, HTP 11642 late juvenile stage. X 2.7. (Photographs by Mr. Ted Piecko.)

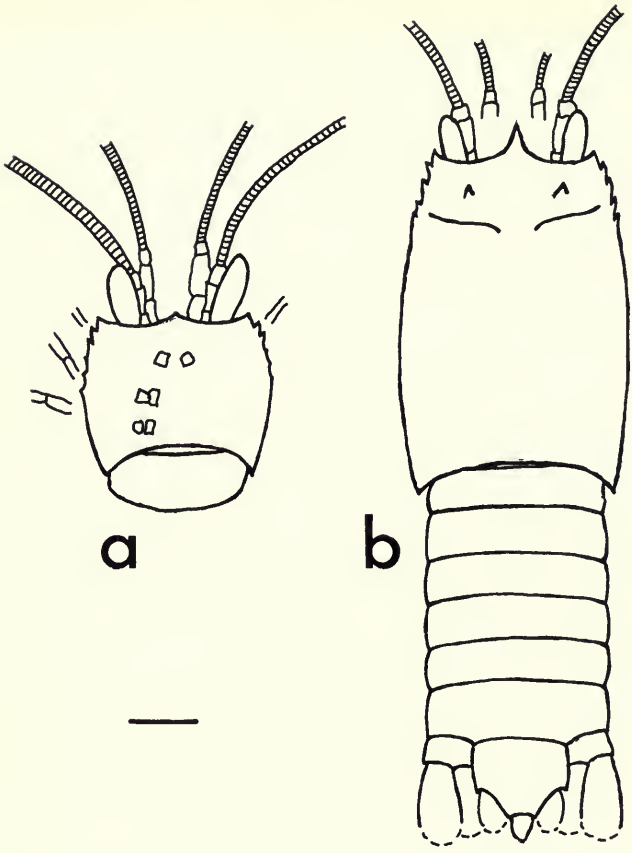

FIG. 15. *M. jaskoskii*. Partial reconstructions of specimens photographed in Figure 14. Scale indicates 1 mm.

inter-relationships of these important elements in the Late Paleozoic radiation.

It is my distinct pleasure to name this species in honor of my former teacher, advisor, and "boss," Professor B. J. Jaskoski of Loyola University of Chicago.

Holotype.—PE 11361 in the collections of Field Museum of Natural History (fig. 4).

Anthracaris gracilis (Meek and Worthen) 1865

Anthrapalaemon gracilis Meek and Worthen, 1865, Proc. Acad. Nat. Hist. Philadelphia, p. 50; 1866, Geol. Survey Ill., 2, p. 406; 1868, Amer. Jour. Sci., **46** ser. 2, p. 554; White, 1884, Indiana Dept. Geol. Nat. Hist., 13th rept. (1883) Palentology, p. 180; Packard, 1885, Amer. Nat., **19**, p. 135; Van Straelen, 1931, Fossilium Catalogus, Animalia, pt. 48, p. 24.

FIG. 16. *Anthracaris gracilis*. YPM 20022 ventral view of thorax with sternites (s), coxa (c), basis (b), endopods (en), and exopods (ex). X 7.

Anthracaris gracilis, Brooks, 1962, Bull. Amer. Paleo., **44**, p. 173; Forster, 1967, Neu. Jahrb. Geol. Palaontol. Abhandl, **128**, p. 186; Brooks, 1969, Treatise Invert. Paleo., Part R (Arthropoda, 4), p. 345; Schram, 1969, Fieldiana: Geol., **12**, p. 219.

Remarks.—Brooks (1962) presented a complete morphologic study of this species. His observations were based on material from the Braidwood fauna collected over a period of years by different people and deposited in

FIG. 17. *Mamayocaris jepseni*. USNM 133393 (holotype) ventral view of thorax with coxa (c), basis (b), endopod (en), and exopod (ex). X 9.5.

various eastern museums. This present study has little new anatomical data concerning *A. gracilis* to add to that excellent work by Brooks. From study of Brooks' monograph and material available to me it appears that *Anthracaris* has an arrangement of mouth parts similar to that described above for *M. jaskoskii*, i.e., large gnathobasic maxillae followed by two maxillipeds. Brooks' interpretation of the pygocephalomorph protopod is questioned below.

Some observations of possible paleoecological importance can be recorded. Just as *Mamayocaris jaskoskii* is apparently characteristic of the

Essex fauna, *Anthracaris gracilis* is practically missing from the Essex fauna. After having inventoried thousands of Mazon Creek shrimp in various private collections in the Chicago area, apparently only two possible *A. gracilis* were found in Essex fauna material. One is in the collection of Mr. Francis Tully of Lockport, Illinois. The other specimen is PE 21904. These specimens are quite small, towards the lower end of variation of this species as given by Brooks.

Certainly *Anthracaris gracilis* can then be said to be indicative of the Braidwood fauna, indigenous to the fresh-water facies of the Mazon Creek

FIG. 18. *M. jepseni*. USNM 133393, counterpart of Figure 17. X 9.5.

area, whereas *Mamayocaris jaskoskii* occupied a more marine facies.

According to Brooks, a prime characteristic of the eocarids is the unsegmented protopod, which he termed "sympod." Actually, very few specimens of any pygocephalomorphs effectively preserve the complete walking legs. Reference has already been made to *M. jaskoskii* material. The point where the exopod articulates with the leg is only partially preserved on a few specimens of *A. gracilis* and the holotype of *M. jepseni*. YPM 20022 (fig. 16) has the exo- and endopods of the third, fourth, and fifth walking legs imposed on each other, but the exopod is seen to articulate with the second segment. YPM 19979 has the distal portion of the exopods preserved and interpolation of missing proximal portions based on the position and direction of the preserved segments would place the point of articulation of the exopod with the second segment of the leg. The holotype of *M. jepseni*, USNM 133393, (figs. 17, 18) clearly preserves the exopods on the second and third walking legs and these can be seen (especially on the third) to articulate with the second segment of the leg. It would appear from these specimens that the protopod of these legs has two segments, a coxa and basis, the exopod articulating with the second, basal segment, and that the endopod apparently has four segments. It would appear Brooks was mistaken in his reconstruction of pygocephalomorph walking legs.

Superorder EOCARIDA Brooks 1962

Order EOCARIDACEA, Brooks 1962

Typical caridoid; thorax somewhat reduced; caudal furcae on telson.

Family BELOTELSONIDAE new family

Antennae well developed; very long rostrum; carapace smooth with incipient development of the branchiostegal area; thoracic sternites present; reptant-type thoracopods lacking exopods.

Belotelson Packard 1886

Diagnosis.—The characters of the genus are the same as those of the family.

Remarks.—This is the most abundant of all the Mazon Creek arthropods. Remains of both dead animals and cast off exoskeletons are recognized. This genus is recognized from several localities in the Carboniferous. *Anthracophausia traquairi* (Peach, 1882) is a species of *Belotelson* (H.K. Brooks, pers. comm.) found in the British Coal Measures of the Lower Carboniferous. *Belotelson* has also been discovered in the uppermost Mississippian or lowermost Pennsylvanian Bear Gulch fauna in Central Montana. *Belotelson magister*, besides being an integral

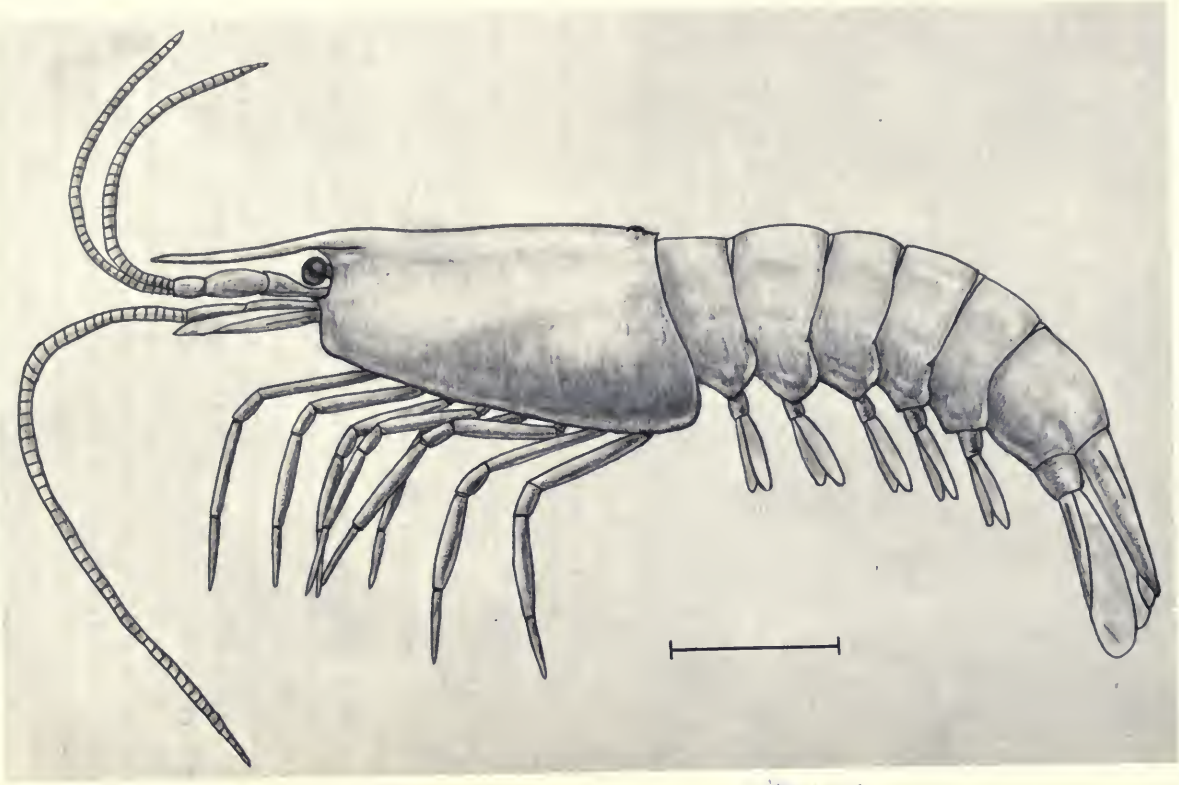

FIG. 19. Lateral reconstruction of *Belotelson magister*. Scale represents 1 cm.

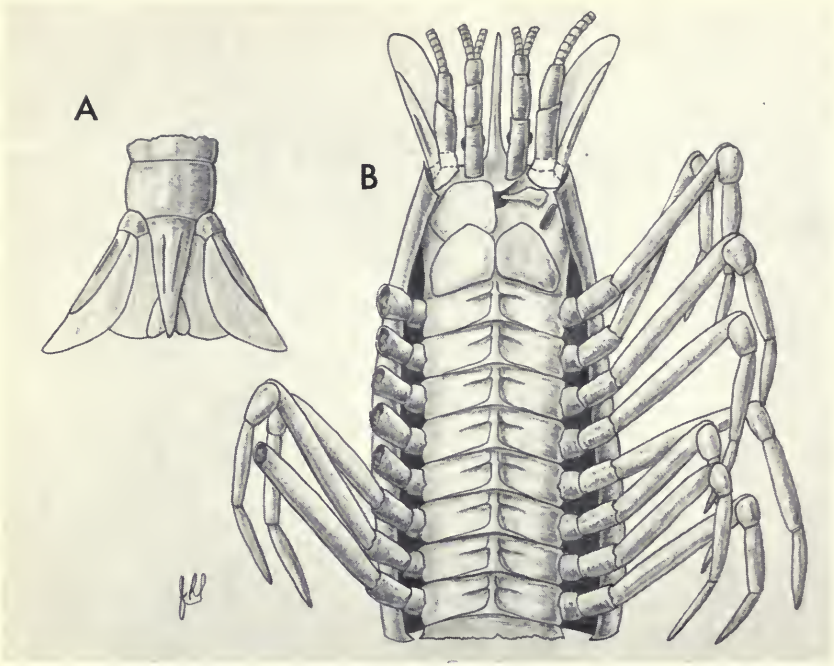

FIG. 20. **A**, reconstruction of tail fan of *B. magister*. **B**, reconstruction of the ventral thorax of *B. magister* with the gnathobase of the left first maxilla removed to expose the mandible. (Leg bases very uncertain.)

constituent of the Mazon Creek Essex fauna, is also found in concretions of the Francis Creek shale in the Sunspot Mine, north of Astoria, Illinois, in Fulton County; in concretions from a strip mine one mile north of Summum, Fulton County, Illinois (one specimen, MS 3903, in the collection of Mildred Scheffel, Peoria, Illinois); from a road-cut of Interstate 80 near Atkinson, Henry County, Illinois (a tail fan, HA 00880, in the collection of Helen Ascher, Peoria, Illinois); in concretions in an abandoned strip mine area near Toluca, Marshall County, Illinois; and some *Belotelson* exuviae are known from an abandoned mining area south of Petersburg, Indiana, in Pike County, Shelbourn Formation (in the collection of Cynthia Miller of Wilmington, Delaware).

The type species, *Belotelson magister* (Packard 1886), had been known from only three specimens collected years ago from the Mazon Creek area in Grundy County, Illinois: USNM 38844 (401a, b) USNM 3884 (401c), and PE 88. In the course of this study a fourth previously unidentified museum specimen from the type locality of *B. magister* was found, USNM 162069. But literally thousands of specimens have been collected from the Essex fauna localities and a definitive reconstruction of this species can now be presented (figs. 19, 20).

Belotelson magister (Packard) 1886

Acanthotelson (?) *magister* Packard, 1886, Mem. Nat. Acad. Sci., **3**, p. 127.
Belotelson magister (Packard), 1886, Mem. Nat. Acad. Sci., p. 128; Van Straelen, 1931, Fossilium Catalogus, Animalia, pt. 48, p. 13; Brooks, 1962, Bull. Amer. Paleontol., **44**, p. 206; Schram, 1969, Fieldiana: Geol., **12**, p. 218; Brooks, 1969, Treatise Invert. Paleontol., Part R (Arthropoda, 4), p. 343.

Description.—Moderate to large caridoid. The carapace is smooth. The long somewhat falciform rostrum arises from the carapace as a mid-dorsal carina and is equal to one-third or one-half the length of the carapace itself (PE 11394). The anterior margin of the carapace has an optic notch to accommodate the stalked compound eyes (PE 21560, fig. 21). A peculiar mid-dorsal foramen (PE 21558, fig. 21) is located near the posterior margin of the carapace (first pointed out to me by Mr. S. LeMay).

The first antenna has a peduncle of three large segments (PE 11252), followed by two well-developed annulate flagella (D 8127, fig. 22). The second antenna has a large exopodal scale almost equal in length to the antennular peduncle. The peduncle of the antenna appears to consist of three segments, the proximal two being relatively small with the distal-most segment being very large (PE 11232). Attached to this is a single, well-developed flagellum. The spherical stalked compound eyes are moderate in size (PE 12415, fig. 23).

The mouth parts consist of a pair of mandibles located behind a labrum and two pairs of maxillae (D 8127, fig. 25). The coxae of these maxillae are quite large and apparently developed as gnathobases and overlie in part the mandibles and area around the mouth. The thoracic legs are developed for reptant habits (PE 12851, PE 16371, see plate 1). The exact identity of the appendage segments is obscure since the basal-most segments lie underneath the thorax and due to the vagaries of preservation are not ordinarily visible. On PE 13718 (fig. 26), PE 21915, and K 11-0133, two of the few specimens which preserve (though very poorly) the proximal leg segments; there are two short segments followed by a very long segment. After the knee, a small carpus proceeds a long propodus and a moderately long dactylus. No exopodal structures have ever been observed in the thousands of specimens seen by this author to date and it is probable that they do not exist, a condition reminiscent of the recent reptantians. A frequent position of preservation is of the ventral surface of the thorax. A herring-bone arrangement of ridges can be seen on the sternites (D 8127, see fig. 24) marking the sternal borders with shorter ridges about half way along the sternal lengths. From such specimens it can be assumed that there probably was at least a slight development of a thoracic endoskeleton, again not unlike the modern reptantians.

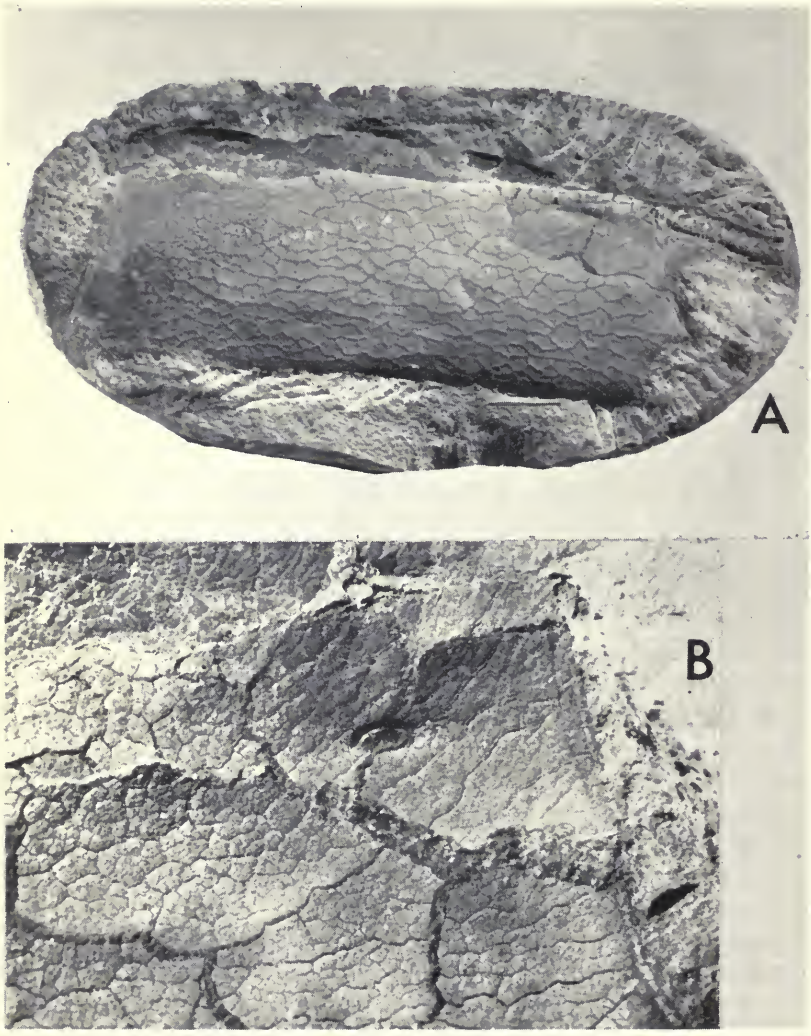

FIG. 21. *B. magister*. A, PE 21560, carapace with base of rostrum and optic notch. X 2.6. B, PE 21558, slightly distorted carapace with posterior, mid-dorsal foramen. X 14.

The abdomen is large and well developed, about equal in length to the thorax. A few specimens have been preserved with the pleopods (PE 8505, fig. 27; PE 16132, fig. 29). The appendages are reminiscent of the swimmerets in some of the modern forms, i.e., a unisegmental base to which are attached the paddle-like exopod and endopod. The tail fan of this species does not bear out the name originally given to the genus. The tail has actually a large, delicate, fan-tail arrangement (D 8201, fig. 28).

FIG. 22. *B. magister.* D 8127, typical fossil type with ventral view of thorax and lateral view of abdomen. X 1.3. (Photo by Field Museum)

The telson is a marked triangular structure to which two small caudal lobes are attached at its distal most end. Whether a caudal spine was located at the tip or not is difficult to determine. The exopod of the uropod is composed of a well sclerotized outer margin which served as a brace for a large membranous lobe. The uropodal endopod was also membranous. The exo- and endopods of the uropod articulate with a well-developed, unisegmental base. The entire effect of the tail, when fully unfolded, was that of a large membranous fan. (This membranous tail fan was apparently quite diaphanous and frequently not preserved.)

Remarks.—A separate family is here erected for *Belotelson*. Brooks (1962) placed this genus in his family Anthracophausiidae as a temporary expedient. He remarked that with only three poorly preserved specimens no meaningful observations could be made as to the anatomy or taxonomic position of *Belotelson magister* at that time. It can now be seen that the obviously reptant nature of *Belotelson* with well-developed

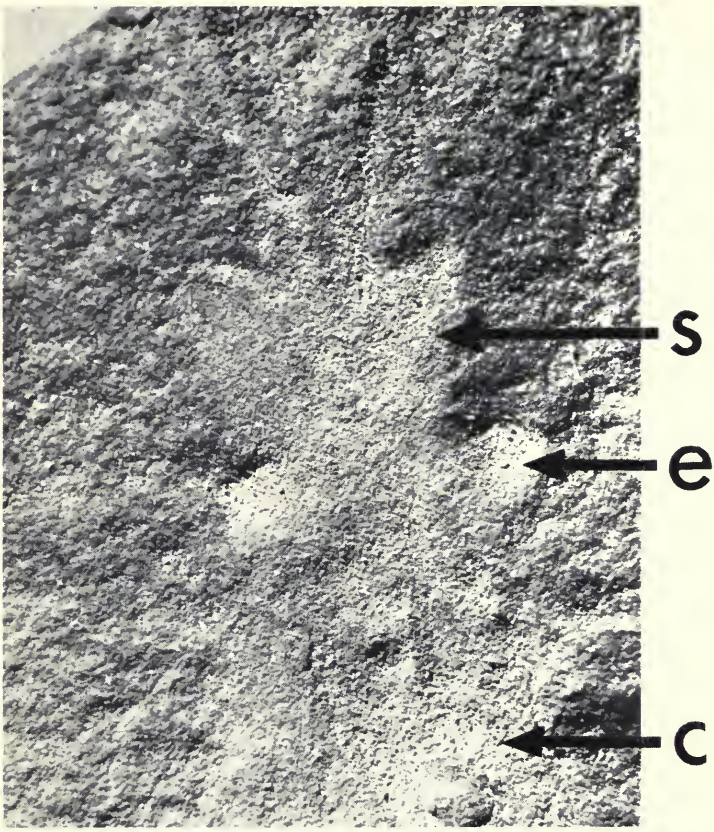

FIG. 23. *B. magister.* PE 12415, a common ghost-like preservation with fossil visible as a color difference in the concretion. Scale of second antenna (s), compound eyes (e), and region of carapace (c). X 5.5.

thoracic sternites easily distinguishes this form from the small natant genera *Anthracophausia* and *Crangopsis. Belotelson* is so distinctive that one might argue against placing it in the Eocaridacea. The walking legs, developed branchiostegite, gnathobasic mouth parts, and large antennae are similar to conditions seen in the pygocephalomorphs. The entire issue of eocaridacean relationships is so confused at this time, however, that it is best to leave the belotelsonids in the eocaridaceans.

Statistical data for *Belotelson magister* are given in Table 2. The high values for the variance for body and carapace length are probably due to age mixture. Though *B. magister* is a common species in the Essex fauna, the number of specimens from which good measures can be obtained is not high. Consequently, specimens with great ranges in size were used.

Animals with a carapace of 1.24 cm. or even smaller are readily recognized as being *B. magister* and conspecific with such large animals as those which had a carapace of 4.5 cm. or larger. If the sample were

TABLE 2. Statistical data for various body measures (in centimeters) of *Belotelson magister*.[1]

	N	$\bar{x}$	s	Range	V
Carapace length	35	2.10±.12	.71	1.24-4.50	23.8
Rostrum length	26	1.36±.09	.46	.68-2.67	33.8
Body (optic notch to telson base)	12	3.32±.24	.84	2.26-4.88	25.3

[1]The significance of the high V is discussed in the text. These are based on measurable specimens collected in Pit 11 in the collections of Field Museum and Eastern Illinois University.

large enough to be able to detect various molt stages, and statistics then calculated for each stage, the variance would probably be more normal. The very high variance for the rostrum is undoubtedly due in part to this age factor.

The function of the posterior mid-dorsal pore on the carapace is unknown. There is no analog to this structure in the modern Malacostraca. It is too small to be used in setting up respiratory currents in the branchiostegal chamber. It might have accommodated a large spine.

From the anatomy and the general form it would appear that *Belotelson* was probably not unlike some of the modern lobsters or crayfish, i.e., a low-level carnivore or scavenger. The well-developed walking legs and antennae would seem to point to a primarily bottom-dwelling existence in which well-developed sensory abilities were necessary. It is interesting to note that in conjunction with the adaptation to a reptant habit the endoskeletal system must have undergone some development. The herring-bone arrangement of ridges on the sternites alluded to above probably mark areas of ingrowth of apodemes for muscle attachment. Such external manifestations of internal structure are noted in modern decapods. The "apodemes" of *Belotelson* interestingly would delineate anterior and posterior chambers within segments which probably accommodated a promotor and remotor musclature used to operate the proximal-most segment of the leg. This also is similar to what takes place in the reptant decapods although the condition in *Belotelson* is not nearly as elaborate.

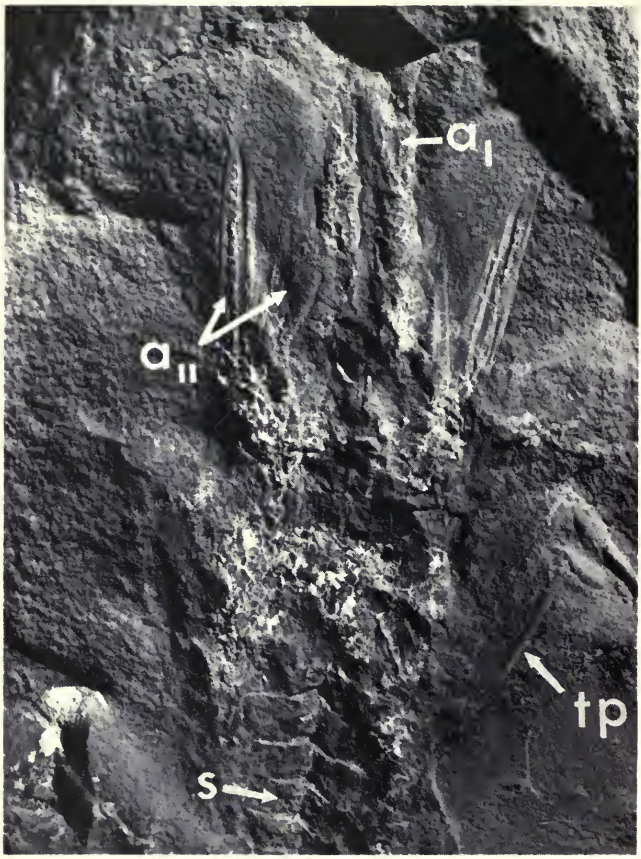

FIG. 24. *B. magister.* An unnumbered specimen out of one of the Chicago area amateur collections showing first antenna (a_I, scale and part of peduncle of second antenna (a_{II}), part of a thoracopod (tp), and thoracic sternite (s). (Photo by Field Museum.)

The most abundant remains of *Belotelson magister* appear to be cast-off exoskeletons (fig. 29). These characteristic and numerous fossils are easily recognized and are frequently called "feather fantails" by the amateur collectors of the Essex fauna. Examination of "thousands" of these fossils has led the author to conclude that they are exuviae of *Belotelson*. The character of the tail fan and the ventral thoracic region verify this. The specimens frequently are collapsed and doubled-up as happens with modern exuviae. A great deal of absorption of minerals out of the exoskeleton of *Belotelson* must have occurred prior to ecdysis. The remains of "living" *Belotelson* are typically well-sclerotized and mineralized, whereas the exuviae are very delicate and preserved as ghost-like silhouettes of lighter color than the concretion matrix.

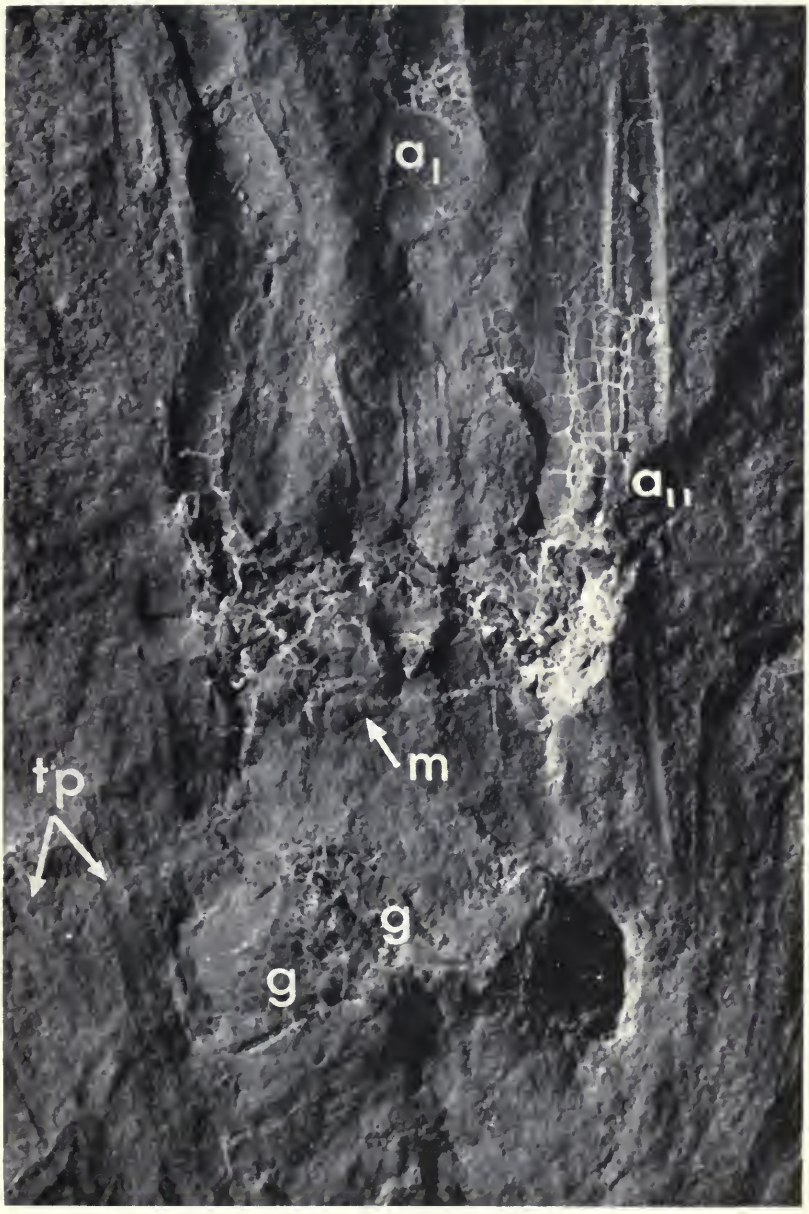

FIG. 25. *B. magister.* D8127, close-up, with first antennal peduncle (a_I), second antenna (a_{II}), mandible (m), parts of thoracopods (tp), and the gnathobases of the maxillae (g). X 8. (Photo by Field Museum.)

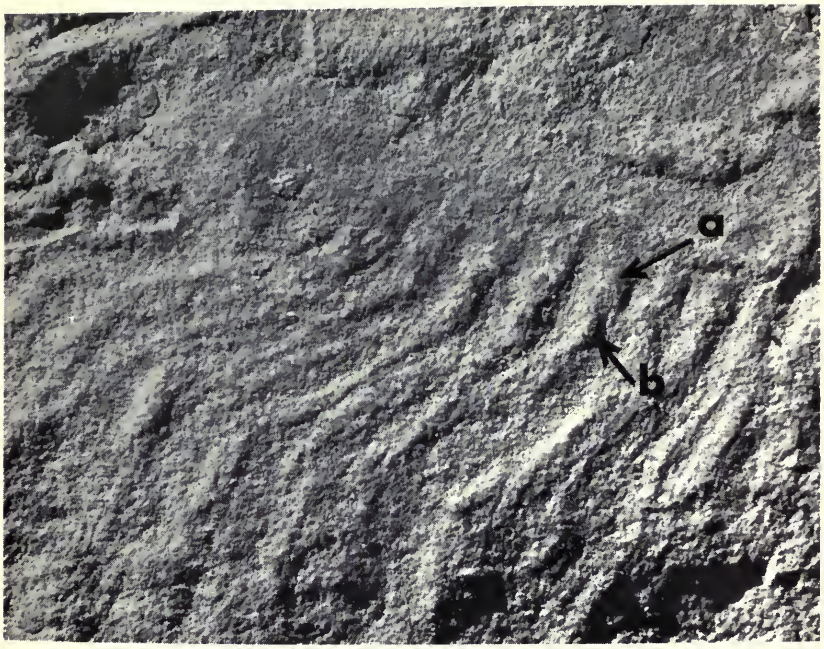

FIG. 26. *B. magister*. PE 13718, lateral view of thorax with the two proximal most segments designated (**a** and **b**), X 5.

It is peculiar that *Belotelson* exuviae are so common, while exuviae of other Essex shrimp are quite rare. Exuviae of *Kallidecthes richardsoni* Schram 1969, have been recorded, and possible exuvial remains of *Mamayocaris jaskoskii* and *Peachella strongi* have been seen. But none of these are as numerous as the exuviae of *Belotelson*.

Family ANTHRACOPHAUSIIDAE, Brooks 1962

Anthracophausia, Peach 1908

Rostrum prominent, but not extremely large; no carinae or branchiostegal keels on carapace; thoracopods natant; point of abdominal flexion the second pleura.

Remarks.—Examination of the type material for *Anthracophausia*, Peach 1908 from the British Lower Carboniferous reveals a taxon with several separate constituents. Without getting too deeply into this matter at this time, it is sufficient to point out that the morphology of *Anthracophausia dunsiana*, the type species, is of such a nature that it does not allow *A. strongi* to be included in the genus *Anthracophausia*. Consequently, *Anthracophausia strongi*, Brooks 1962 must be placed in a separate new genus.

Peachella, new genus

Diagnosis.—Rostrum moderate in size and keeled; all abdominal pleura similar and broadly rounded; caudal lobes small and located disto-laterally.

Type species.—*Peachella strongi* (Brooks) 1962

Peachella strongi (Brooks) 1962

Anthracophausia strongi Brooks, 1962. Bull. Amer. Paleo., **44**, p. 202; Brooks, 1969, Treatise Invert. Paleontol., Part R, (Arthropoda, 4), p. 342; Schram, 1969, Fieldiana: Geol., **12**, p. 218.

Diagnosis.—Rostrum straight and pointed; pleural lobes are broadly rounded.

Remarks.—This species was described by Brooks, (1962) on the basis of two specimens of very fine preservation collected in the 1800's by A. A. Strong for the Yale Peabody Museum. Although *Peachella* is a fairly common crustacean in the Essex fauna, it is almost always subject to inferior preservation at that locality. Very few specimens of this species from the Essex fauna can be favorably compared to the types (fig. 30). Some additional information on the anatomy of *P. strongi* has been revealed, however, by the Essex fauna material.

FIG. 27. *B. magister*. PE 8505, lateral preservation with thoracopods and pleopods visible. X 2.8.

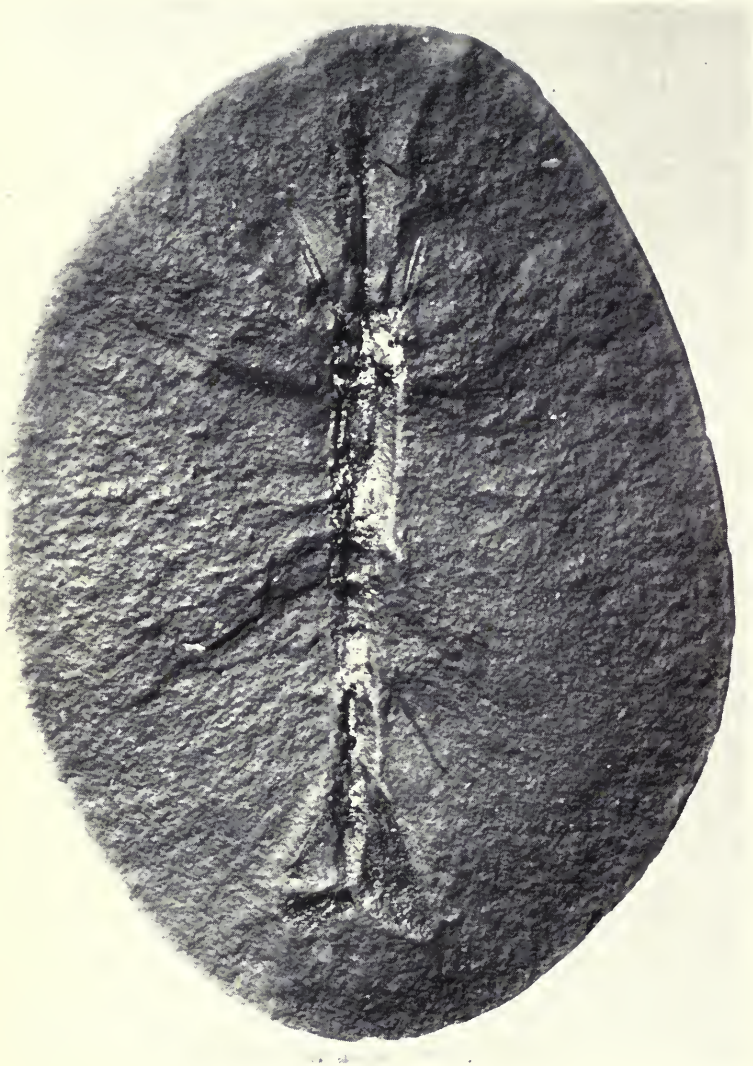

FIG. 28. *B. magister*. D 8201, dorsal preservation with tail fan. X 2. (Photo by Field Museum.)

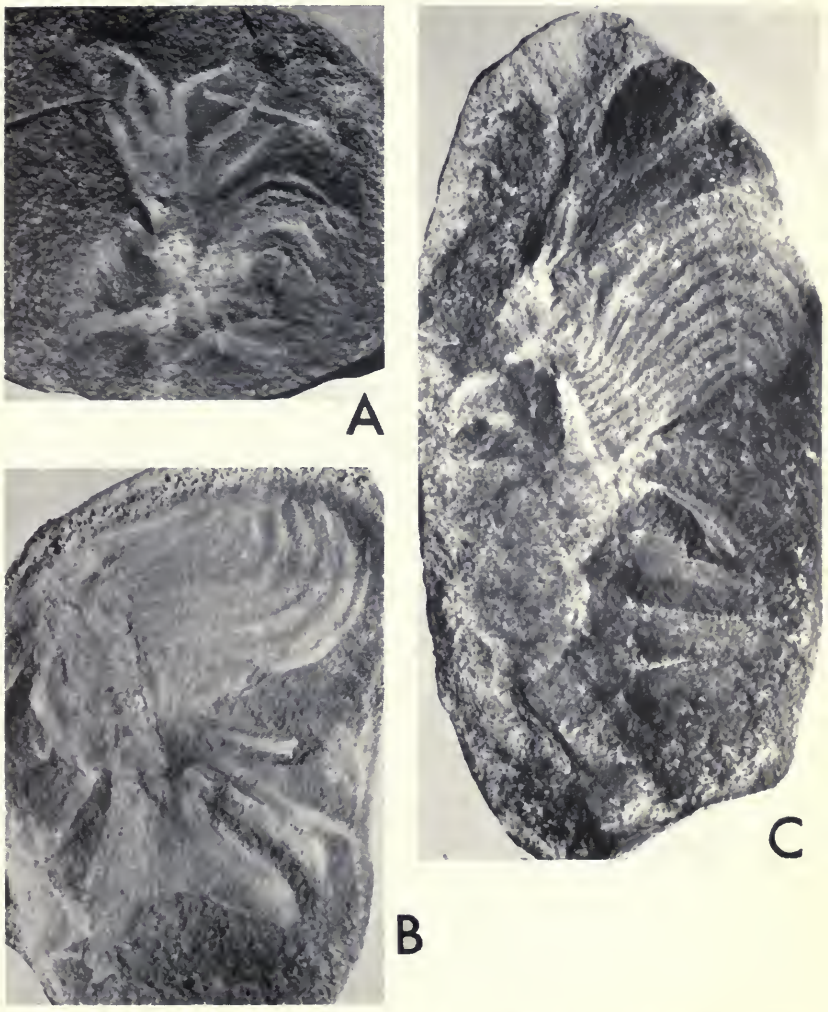

FIG. 29. *B. magister*. Various fossils of possible exuviae (cast-off exoskeletons) preserved largely as color differences on the concretion. **A**, PE 12535. X 1.6. **B**, PE 11388. X 1.6. **C**, PE 16132. X 1.7.

The stalked compound eyes are relatively large in size and spherical (PE 10856, fig. 31). The flagella of the antennae are about equal in size and are about as long as the dorsal midline of the carapace (PE 13169, fig. 31). Exopods of the thoracic appendages are indicated on several specimens but the preservation is very poor (I have reconstructed them as typical caridoid annulate exopods). The pleopods (PE 12993, fig. 32) have a protopod of one or two segments and flap-like endopods and exopods. The

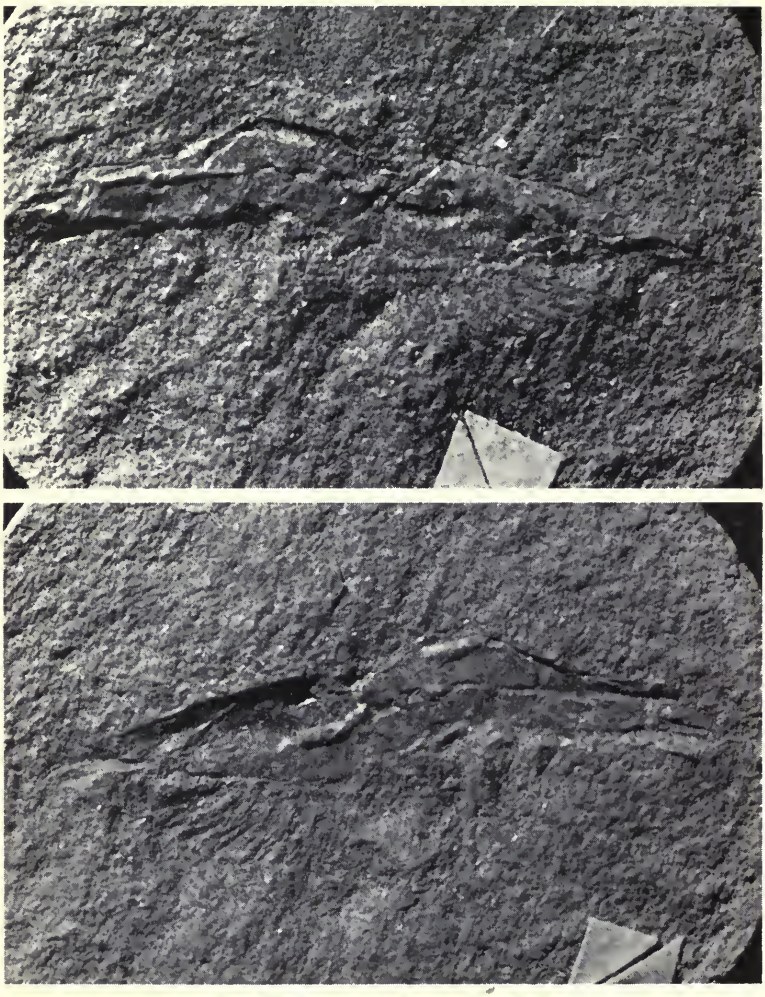

FIG. 30. *Peachella strongi*. YPM 18821, Holotype. X 4.

nature of the tail fan is still obscure. The broad exopod and endopod of the uropod are apparent on the Essex specimens but no clear concept of the telson could be developed. Preparation of the holotype seemed to indicate laterally placed caudal lobes but again poor preservation has intervened.

A reconstruction is offered in Figure 33.

The Essex *Peachella* are typically ghost-like in preservation. The lighter outline of the fossil material is readily seen against the darker matrix of the concretion but details fade out under microscopic study.

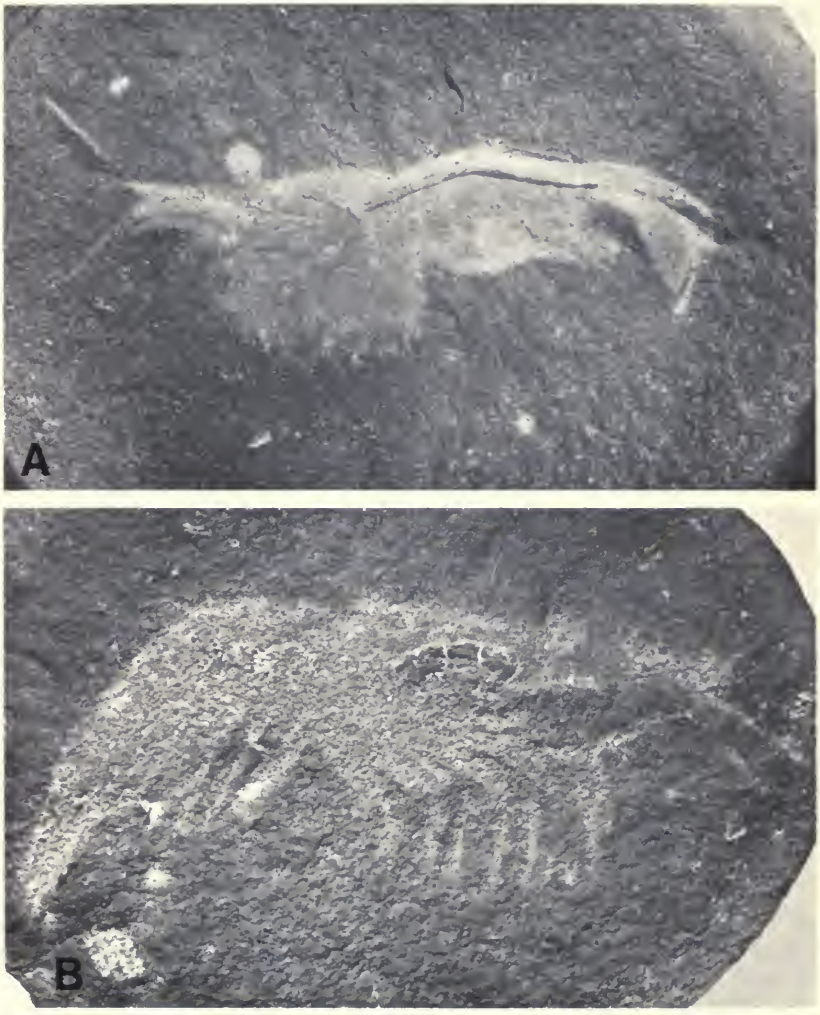

FIG. 31. *P. strongi*. **A**, PE 10856, with stalked compound eyes. X 2.6 **B**, PE 13169, typical ghosty type of preservation (a color outline on the concretion) of this species with parts of a detritus-filled gut and various appendages preserved. X 3.5.

Family ESSOIDIIDAE, new family

Point of flexion for the abdomen at the first pleomere.

Essoidia, new genus

Diagnosis.—Small, natant eocarid; carapace rectangular in outline with optic notch; rostrum small and pointed; no grooves or sculpturing on

FIG. 32. *P. strongi.* PE 12993, with pleopods. X 2.5.

the carapace; first antenna with three large peduncular segments; second antenna much smaller than the first; abdomen equal in length to the cephalothorax; first abdominal segment enlarged to facilitate flexure; uropods with blade-like exopods and endopods; telson rectangular with a pair of terminal caudal lobes and a small pointed, posterior projection of the telson between them.

Type-species.—Essoidia epiceron Schram, n. sp.

Remarks.—This small crustacean is found in moderate numbers in collections of the Essex fauna shrimp. It is apparently subject to clustered distributions within Pit 11, the principal Essex fauna locality. Some collectors have accumulated large numbers of this species in their collections, others have hardly any, depending on where and how individuals collect specimens. The preservation is usually good, except for the legs which were apparently delicate and perishable.

Essoidia epiceron, new species

Diagnosis.—Since but one species is known, the diagnosis of the species is the same as that of the genus.

Description.—This little shrimp is approximately 14 mm. from the tip of the rostrum to the tip of the telson. The carapace is rectangular in outline, and was not attached to at least the posterior thoracomeres. A

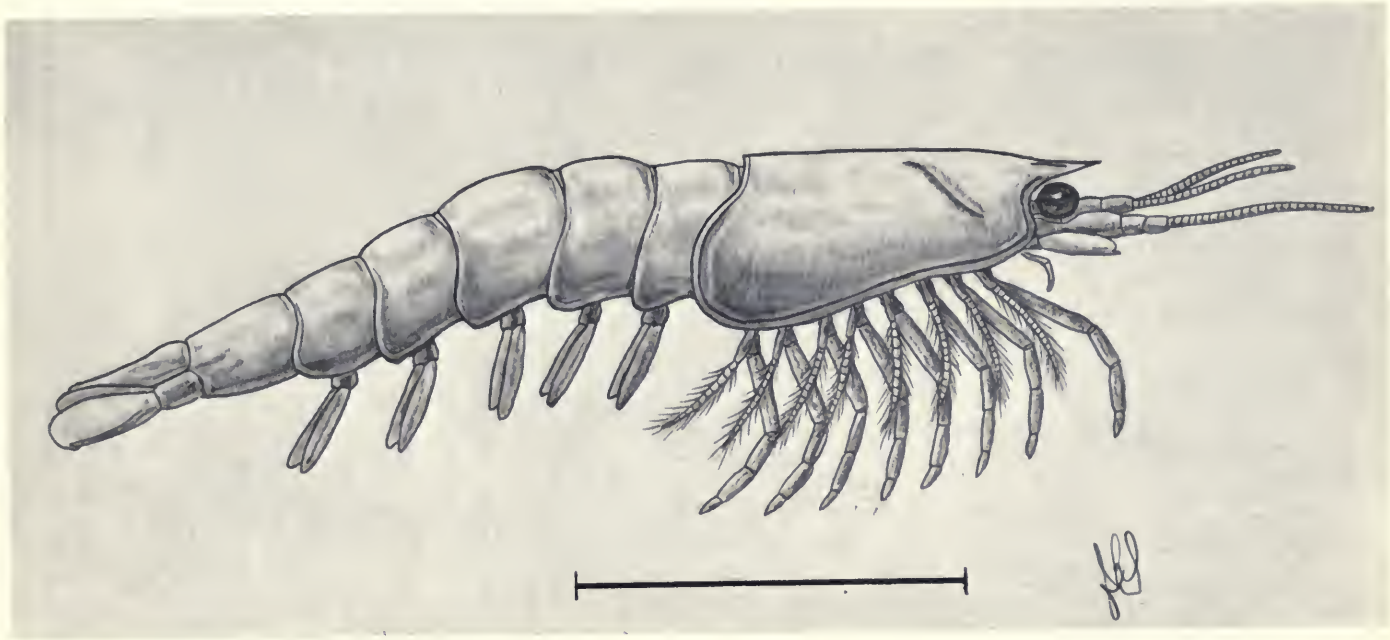

FIG. 33. *P. strongi.* Modified from Brooks (1962), modifications based on Essex fauna material. Scale represents 1 cm.

FIG. 34. *Essoidia epiceron*. PE 12211, close-up of carapace displaying rostrum (r) and optic notch. Arrows delineating the carapace margin. X 16.

doublure is present along the margins. The carapace surface is smooth. An optic notch is on the anterior margin (PE 12211, fig. 34). The rostrum is short and pointed.

Complete thoracic appendages have not been observed on any of the specimens examined to date. PE 12211 preserves parts of the proximal two segments on the posterior thoracomeres. The proximal segment (a protopod or sympod?) is quite short and this is followed by part of a longer segment. K 11-0134 (fig. 35) obscurely displays the short protopod, the long ischium, and traces of the other segments. This latter specimen indicates that the thoracopods of *E. epiceron* were long and delicate.

The first antennal peduncle has three segments. The proximal segment is short and narrow, the second is considerably longer and expanded distally, the third is shorter again, wide, and projected anteriorly along its

ventral margin (PE 10475). The narrowness of the first segment and the proximal portion of the second appear to form an optic groove. PE 10475 has part of the peduncle of the second antenna, but it is poorly preserved and the exact nature of this appendage cannot be determined. No flagella have been preserved on any of the specimens examined.

The abdomen is about equal in length to the cephalothorax. The first segment is unusual in that it is the permanent point of flexure. It is quite enlarged over the following segments and formed dorsally in such a manner that the animal is permanently bent at that point (PE 13263, fig. 36; G 061-113). The remaining pleomeres are about equal in size and each overlaps its posterior neighbor with a smooth, round lappet. No pleopods have been observed.

The uropods are composed of blade-like endopods and exopods (PE 12221). The telson is subrectangular and has a posteriorly directed process along its hind margin. On this margin and lateral to the pointed process are a pair of caudal lobes (PE 12209 and PE 13264). The edges of the telson from its base to just in front of the caudal lobes are serrated (PE 13469 fig. 37).

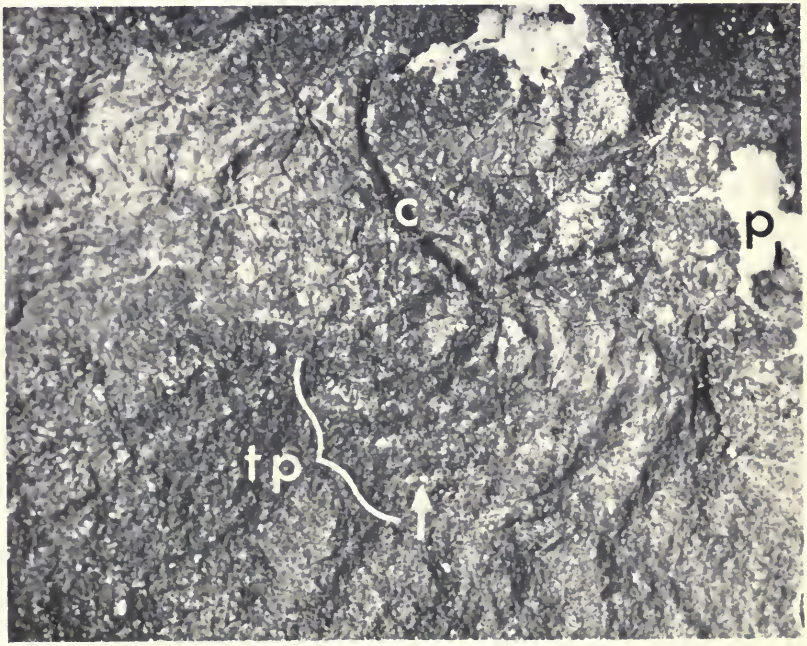

FIG. 35. *E. epiceron.* K11-0134, close-up with the carapace (c), the faint, delicate proximal segments of the thoracopods (tp), and part of the first pleomere (p_1). Specimen of inferior preservational quality but one of the few that display the thoracopods in any way. X 16.

A reconstruction of this animal as presently understood is offered in Figure 38.

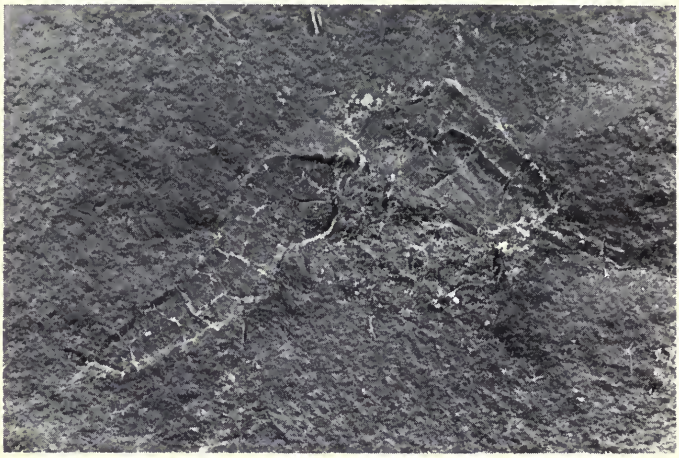

FIG. 36. *E. epiceron*. PE 13263, displaying the sigmoid form of the fossils. Carapace partially lifted off the underlying thoracomeres. X 4.6.

Remarks.—The most unusual aspect of this animal is the manner of flexion of the abdomen. *Essoidia* differs significantly from the genera *Anthracophausia* and *Peachella*. In these latter two genera the abdomen bends at the second abdominal segment (fig. 33) while *Essoidia* bends at the first segment. Not only the point of flexure but the manner of flexure is different as well. *Anthracophausia* and *Peachella* bend by overlapping the pleura and are capable of completely straightening the abdomen. *Essoidia* could not straighten its abdomen since the flexed segment is the first pleomere, difficulty would arise in overlapping the carapace and pleura of the thoracic segments. Consequently, the first segment is structured so as to be permanently bent, directing the distal abdominal segments at an angle of 20-30 degrees from the axis of the cephalothorax. A limited "straightening" of the abdomen was achieved in the fossils only by bending back the terminal segments of the abdomen dorsally. This gives the animal in side view a distinctive "S" shape, from which the generic name is derived.

The exact functional significance of this arrangement is not clear. It may be that the downward thrust of the abdomen associated with the caridoid escape reaction is increased with the dorsally directed extension of the abdomen. Not only would the abdomen be "spring loaded" in this position, the muscles of flexion being quite stretched when in the extended

FIG. 37. *E. epiceron*. PE 13469, close-up of tail fan with parts of the uropods, the telson with its serrated margins, and portions of the caudal lobes. X 16.

position, but the arc of flexure would be increased because of the incipient angulation of the first segment. Thus *Essoidia* might have possessed a very strong, fast caridoid escape reaction.

Another interesting line of reasoning is suggested by the females of the recent mysids, *Bowmaniella* and *Gastrocaccus*. These animals have greatly expanded pleurites on the first abdominal segment (fig. 39) which act to supplement the thoracic brood pouch. The modification of the first abdominal segment of *Essoidia* might be due to such a specialization though all the specimens that preserve this area have the enlarged segment and there appears to be no observable sexual dimorphism.

K 11-0134 and PE 12211 have traces of small, feather-like structures on the thoracic pleura. They are very diaphanous and are observable only under the highest power and low-angle lighting. They resemble the gills seen on animals like *Kallidecthes* (Schram, 1969). They are found only on the pleura and there are no indications of them on any of the leg segments. Thus it would appear that, if these are gills, *Essoidia* is more akin to mysids than to euphausiaceans, which do bear gills on the basal segments of the thoracic appendages.

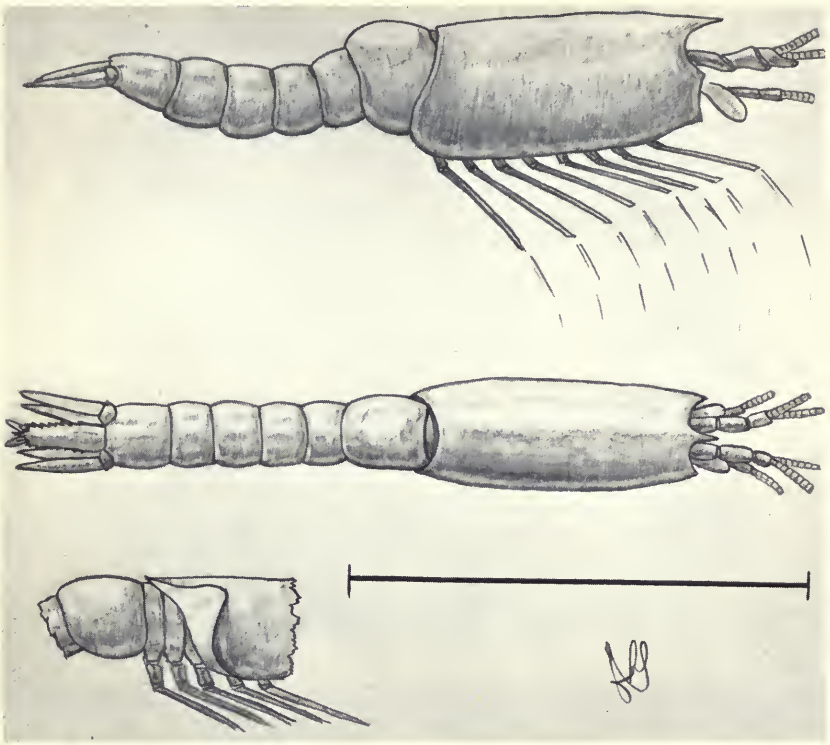

FIG. 38. *E. epiceron*. Partial reconstruction. Scale represents 1 cm.

The tail fan most closely resembles that of the modern Euphausiacea. None of the specimens examined has a caudal spine. The tip of the telson is directed posteriorly as a pointed process but the small size of this species and vagaries of preservation make it difficult to observe. *Essoidia* conforms to the eocarid plan only in having small caudal lobes present. It is possible, however, that the caudal spine has been lost, not unlike the "caudal lobes" observed by Manton (1928) in the juvenile stages of *Hemimysis*. In this regard *Essoidia* would anticipate the condition of the modern "schizopods." The thoracic appendages exhibit adaptations found in modern natantians.

Statistical data for *E. epiceron* is presented in Table 3.

Holotype.—PE 12211 is in the collection of Field Museum of Natural History (fig. 40).

DISCUSSION

The taxonomic assignments of the eocarids have varied through the years. Huxley (1857) described *Pygocephalus cooperi* and termed it an

"early form of decapod" or possibly a stomatopod. Etheridge (1877), in describing some specimens of *Anthrapalaemon*, classified them as macrurous decapods. Whitfield (1892) followed Etheridge and placed

TABLE 3. Statistical data for various body measures (in centimeters) of *Essoidia epiceron*.[1]

	N	$\bar{x}$	s	Range	V
Carapace length	16	.42±.01	.05	.34- .52	11.9
Body (optic notch to telson base)	5	1.19±.04	.10	1.07-1.31	8.1
Telson	12	.21±.01	.05	.10- .28	21.8

[1]The sample of measurable specimens is small and based on material in the collections of Field Museum and Mr. and Mrs. Ted Piecko.

Palaeopalaemon newberryi in the macrurous decapods as well. Woodward (1908) also believed *Anthrapalaemon* to be a decapod but had compared *Pygocephalus*, with which *Anthrapalaemon* is synonymous, with the mysidaceans in 1907.

Peach (1908) in his monographic work on the fossil shrimp of Britain felt that all the Paleozoic shrimp were schizopods, i.e., euphausiaceans or mysidaceans. The genera he placed in the mysids included *Tealliocaris*, *Pseudogalathea*, *Anthrapalaemon*, *Pygocephalus*, and *Palaeomysis*. He also included *Perimecturus* and *Palaeocaris* in the mysidaceans. *Anthracophausia* and *Crangopsis* were placed in the Euphausiacea. Much of Peach's work remained unchanged for some years. Van Straelen (1922) assigned his genus *Anthracomysis* to the mysidaceans. And as late as 1957 Copeland accepted and used Peach's taxonomic assignments unchanged.

In 1962, Brooks, culminating a study of several years, completely redefined the Paleozoic caridoid eumalacostracans. All previous authors had attempted to interpret the Paleozoic fauna as essentially modern in character. They naturally chose to fit these extinct forms into modern taxa. Brooks, however, was able to free himself of this traditional outlook and considered these fossil shrimp in their Paleozoic context. What then became obvious was that elements of the Paleozoic fauna, though bearing a number of superficial similarities to modern groups, were quite distinct in themselves and seemed to be the subject of an elaborate radiation in the Late Paleozoic which was quite separate and distinct from the later Mesozoic and Cenozoic radiations. He believed that the Paleozoic caridoids were all characterized by having an apparently unisegmental protopod, or sympod, on their thoracic appendages. In addition, they

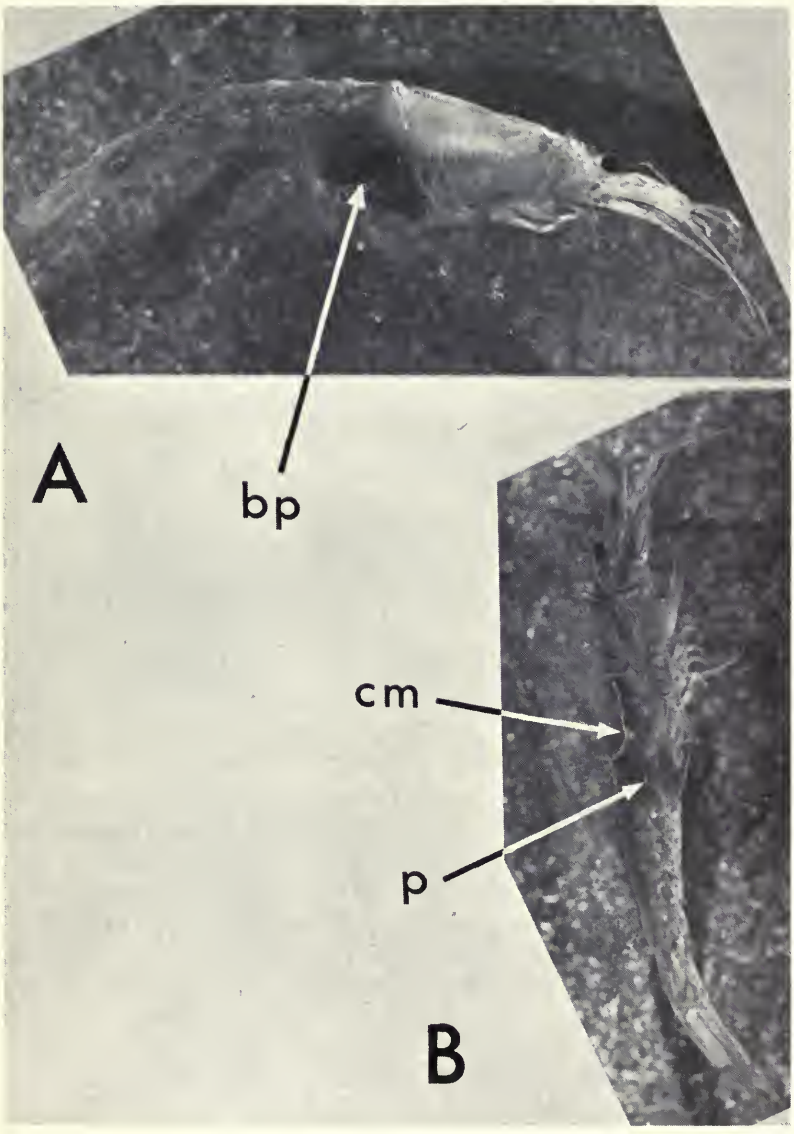

FIG. 39. *Bowmaniella braziliensis* from the recent crustacean collections of the U. S. National Museum. Brood pouch filled with eggs (bp), carapace margin (cm), and inflated pleurites of the first pleomere (p). **A**, lateral view of gravid female. **B**, ventral oblique view of a non-gravid female. X 10.

FIG. 40. *E. epiceron*. PE 12211. Holotype. X 6.7.

bore an elaborate tail fan in which the telson had well-developed caudal lobes and a median caudal spine. Although some forms did seem to possess reproductive structures not unlike the peracarids, (viz., the oostegites on some of the pygocephalomorphs) they were by no means consistent in this regard. Some had a peculiar large opening on the eighth thoracic sternite which Brooks termed a seminal receptacle. Some forms even possessed both oostegites and the seminal receptacle. Thus, although the Paleozoic forms seemed to be quite distinct from those of the later radiation, Brooks felt there were still some puzzling aspects to their anatomy and consequent taxonomy. He felt it better to classify these species in the context of their being entities of the Paleozoic and part of that radiation, and to minimize certain resemblances to the modern fauna while emphasizing their similarities to each other.

Brooks expressed the belief that with more forms and further study a clarification of the relation of the Paleozoic radiation to later forms would be forthcoming. Although more and better material has come to light in the course of the Mazon Creek project, and I have examined all previously available North American eocarids, our understanding of the Paleozoic caridoids still remains clouded.

The nature of the tail fan and the protopod are the only distinguishing features of the eocarids as Brooks recognized them. Tail-fan structure differs between the two eocarid orders of Brooks. The pygocephalomorphs have a well-developed tailfan with marked development of the caudal lobes and spines on the telson. This appears to be a consistent feature throughout the group. The eocaridaceans have a variety of conditions ranging from well-developed lobes in *Belotelson* to very diminutive lobes in creatures like *Essoidia* or perhaps *Peachella*. The caudal spine is not present. In fact, the telson of a form like *Essoidia* is very similar to the arrangement seen in juvenile mysids, i.e., an elongate telson with small, subterminal furcae. One might thus question the importance of tail fan structure in delineating the Eocarida.

The protopodal character is even more dubious. Not one eocaridacean fossil effectively preserves the appendages so that a definite determination of whether the protopod has one or two segments can be made. The only possible exception is *Belotelson* (and here the few specimens that preserve this area are of very poor quality and leave much to be desired concerning clarity). There are only a total of six segments in the telopodite of pygocephalomorph thoracopods. Although Brooks clearly reconstructs the exopod coming off the basal-most segments of the thoracopods, critical examination of this area on the pertinent fossils cannot verify this arrangement. In fact, few specimens of any pygocephalomorphs clearly

preserve this feature. I have examined all of the North American specimens that could enlighten us concerning this feature of the anatomy, and in most cases it was ambiguous. As noted above, however, a few specimens indicate a normal two-segment protopod. The exopods arise from the second segment (or basis) based on the arrangement of structures on these fossils. This would leave an endopod with apparently four segments instead of a normal five. This condition could be due to a fusion of two endopodal segments, not unlike the basiischium which occurs in the decapod eucarids. The third segment on the pygocephalomorph thoracopod is quite long and might easily represent an ischiomerus. No clear seam, as is sometimes detectable on the decapod basiischium, has been observed on this third segment in any of the pygocephalomorph material examined by me. I believe, however, the protopod of these beasts is indeed composed of two segments, a coxa and basis. The nature of this area cannot be determined at this time for eocaridaceans.

We are now confronted with a dilemma. Do we continue, at least for the time being, to use rather uncertain characters to delineate the superorder Eocarida, or do we seek to place these animals in other taxa? For the time being, the first alternative will have to do for the Eocaridacea, but I suspect that we shall end up reassigning these organisms as more information becomes available. The entire issue is clouded by the convergences we see in the Late Paleozoic radiation to anatomical arrangements in the modern fauna.

The pygocephalomorphs superficially resemble "crayfish" or small "lobsters" and have been compared to crabs in some instances. Förster (1967) compares them to his Triassic Erymidae and indicates his belief that the pygocephalomorphs are ancestral to the decapods.

Indeed, the similarity in gross anatomy of the ventral thorax of pygocephalomorphs to living palinurids is striking. The same triangular arrangement of the thoracic sternites is evident (fig. 41), the anterior sternites being the narrowest and the posterior ones the widest. Förster even points out similarities to the seminal receptacles on the Mesozoic forms. Although this convergence is striking, I believe it is just that, a convergence. Pygocephalomorphs have six walking thoracopods while decapods have five; reptant decapods completely lack an exopod; if the nature of the leg segments suggested above holds true, decapods have a basiischium rather than an ischiomerus; the decapods have an elaborately grooved carapace which the pygocephalomorphs lack; the pygocephalomorphs have oostegites (a feature in the living forms seen only in the peracarids); no pygocephalomorph fossils ever exhibit pleopods despite exceptional preservation of the material and I think as a result we must

FIG. 41. Ventral view of the thorax of the recent palinuroidean, *Puerulus* cf. *sewelli*. Note the triangular field of the sternites.

consider the strong possibility they may not have had any; and the pygocephalomorphs did have the elaborate tail fan. Finally, the trend in pygocephalomorph evolution was not toward a "macrurous decapod" but rather toward a crab-like condition. The Permian family Notocarididae reduced the abdomen and carried it flexed under the thorax in the manner of a "brachyurous decapod."

I believe then that pygocephalomorphs have nothing to do with decapod evolution.

The presence of oostegites on the pygocephalomorphs suggests another possible taxonomic affinity, viz., peracarids. Indeed, superficial similarities of pygocephalomorph body shape to the lophogastrid mysidaceans is very close: the oostegites, the carapace, thoracic exopods, even, to some extent, the telson. The notable exceptions are the triangular arrangement of thoracic sternites, gnathic maxillae, and the two pair of maxillipeds in pygocephalomorphs. Such features, however, could be accommodated within the mysidacean peracarids as aberrant, specialized conditions. Pygocephalomorphs are thus best classified as peracarids.

Belotelson is even more strongly prefigurative of modern macrurous forms (perhaps even more than the pygocephalomorphs) with their cylindrical bodies, long walking legs, biramous pleopods, and lack of thoracic exopods. But after considering these characters we are again confronted with an array of unique features. There are eight pairs of well-developed thoracopods which arise from the thorax at a lateral position, i.e., all the thoracomeres have well-developed sternites. The exact identity of the individual segments of the thoracopods is again a mystery. Though there appears to be only a total of six thoracopodal segments, there are some alternatives in interpreting these. Brooks' thesis of a unisegmental protopod may be applied here. Or, as indicated previously, there may be a fusion of segments in the endopod. Again this latter assumption is attractive when one considers that the third segment in the leg is exceptionally long, indicating perhaps an ischiomerus. Since there are no thoracic exopods, it is difficult to assess which alternative may be correct. Within the confines of Calman's (1909) caridoid morphotype the second alternative may be preferable.

When we compare *Belotelson* to modern forms the "lobster-ness" of the animal is obvious. But when we examine the underside of the thorax we see some distinct differences. *B. magister* has well-developed sternites on all the thoracomeres. The palinurids, ("spiny lobsters"), as already mentioned above, have a triangular arrangement of sternites. The astacids (the true lobsters and the crayfish), have their thoracopods originating along the ventral midline (fig. 42), with no sternal development. Indeed, this condition is a primitive one for decapods. The nektonic dendrobranchiates, such as the penaeids; or the nektonic pleocyemates, like the Caridea, also have the thoracopods arising along the ventral mid line. This arrangement can be extended to Anomura like the hermit crabs (*Pagurus*), ghost shrimp (*Upogebia*), or sand crabs (*Emerita*)—all these forms have no development of sternites.

Sternite development in eucarids occurs only in the palinurids and the Brachyura. Indeed, in the dromiacean crabs, the most primitive

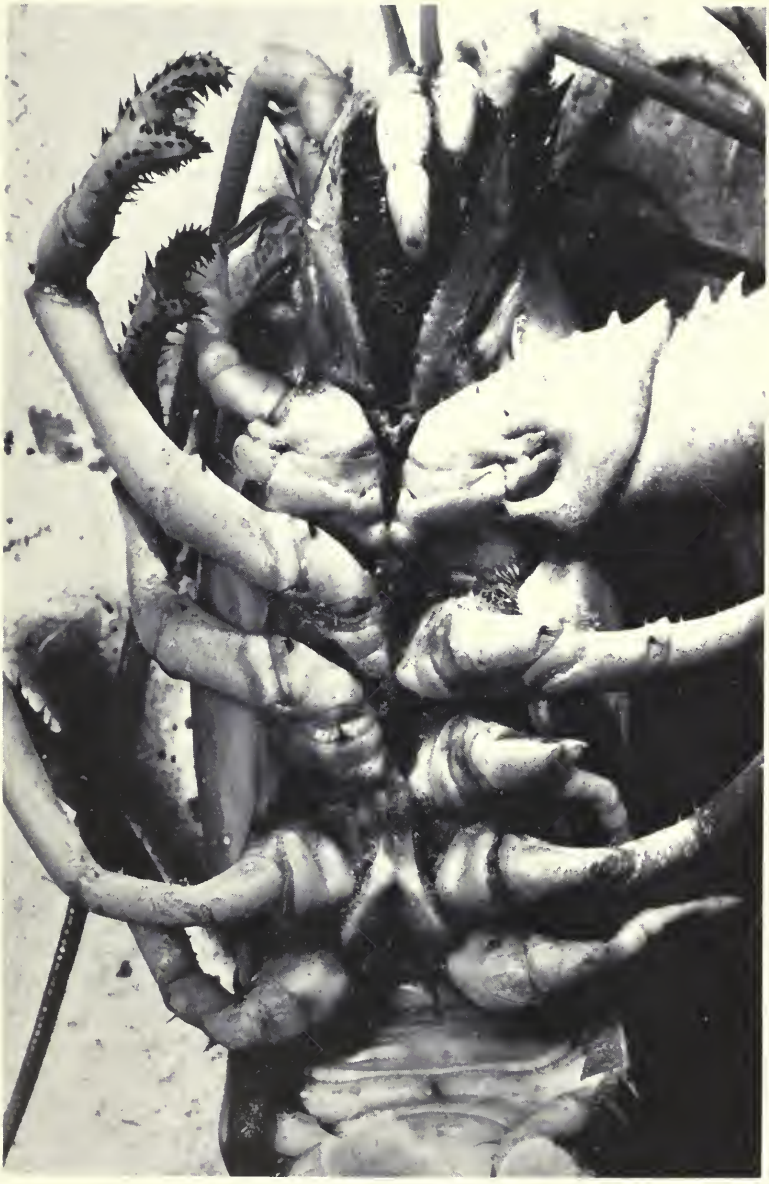

FIG. 42. Ventral view of the thorax of the astacidean, *Homarus americanus*. Note that the thoracopods arise near the mid-ventral line.

brachyurans, the sternites are hardly developed; the thoracopods arise very near the ventral midline. The typical crab arrangement is a specialization, with a broadening of thoracic sternites causing the legs to arise from the sides of the thorax.

Belotelson, then, with its well-developed sternites and lateral origin for the legs, is a very specialized animal, well advanced along the line of evolution. It cannot have given rise to primitive eucarid forms which are generalized in regard to their sternites and thoracopods.

The exact taxonomic affinities of *Belotelson* remain obscure. It does have a well-developed tail fan with caudal lobes, though it appears to lack a caudal spine. None of the thoracopods have become specialized as maxillipeds. (Nor is it likely that any ever did due to the specialized nature of all the thoracic sternites.) The maxillae are present as strongly developed gnathobases. In the course of examining literally thousands of specimens of *B. magister* I have never noted any oostegites, or any specimens with the carapace lifted off the underlying thoracic segments. This is negative evidence but I would be inclined to assume that the species did not have oostegites and the carapace was not unattached as in the peracarids. This latter point may be extremely important. A frequent fossil of *B. magister* is a lateral preservation of the carapace alone. (These separate carapaces are like that which occurs in molting lobsters, where the animal emerges from beneath an intact carapace which lifted up posteriorly to allow the creature to step out of the old exoskeleton.) Unfused and partially dislocated carapaces (in the mode of peracarids) occur for other Essex fauna crustaceans such as *Essoidia*. But we never get lateral preservations of whole *Belotelson magister* with the carapace partially dislocated. The completely separate carapaces are unique and may represent distinctive preservational circumstances. Interestingly enough, all such carapaces come from very large individuals.

The only living group which might be able to accommodate *Belotelson* (with a carapace fused to the segments below, and having eight pairs of walking legs) would be the Euphausiacea. The difficulty in attempting to place belotelsonids here is in the lack of an exopod on *B. magister.* This would not be a serious impediment however. *Belotelson* obviously is a reptant, low-level carnivore. Such animals do not require such a structure.

Essoidia epiceron has the caudal lobes on its telson but no caudal spine. This would qualify it for placement in the Eocarida. But no clear impression can be gained of the nature of the protopods. The distal portion of the thoracic endopod are long and delicate as one expects in a natant filter feeder. The thoracopods in the one specimen that displays this, K11-0134, are not well enough preserved to determine if there is a

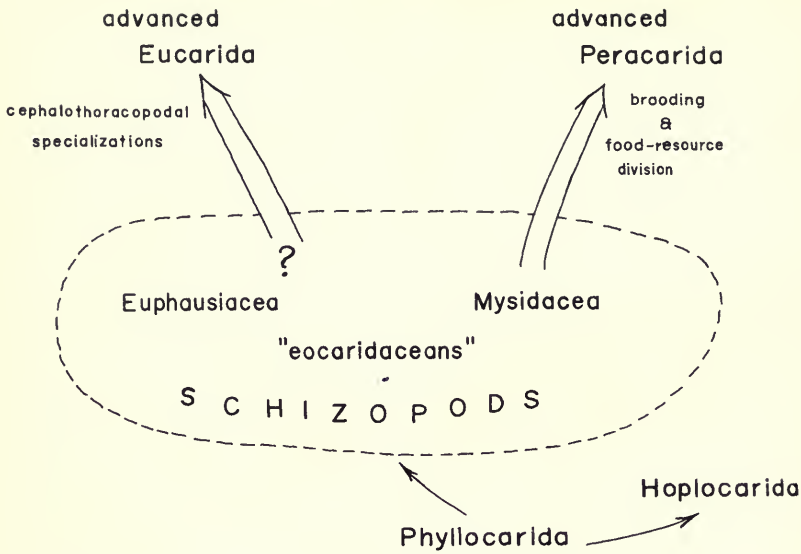

FIG. 43. Phyletic interpretation emerging from the study of Late Paleozoic caridoid Eumalacostraca. Caridoids arose from Phyllocarida as a rather diverse yet primitive group, the "schizopods." Within the schizopods two groups are clearly recognized, the Mysidacea, with peracarid affinities, and the Euphausiacea, with eucarid affinities. In addition to these two, a rather indistinct assemblage of Late Paleozoic, caridoid families, the eocaridaceans of Brooks, occupy a position somewhere between the two clearly delineated orders. From the schizopods developed two major radiations, each on a rather broad front. The advanced peracarids arose from the mysidaceans. The advanced eucarids arose from either euphausiaceans or, perhaps, from somewhere in what are now termed eocaridaceans.

one or two segment protopod. It is conceivable that *Essoidia* could be accommodated in the mysid, mysidacean peracarids.

Peachella strongi occurs very rarely and then typically in very poor preservations. In general, the same comments offered on *Essoidia* could also apply here.

A clearer image of the Late Paleozoic caridoid radiation now emerges. There were strictly natant, filter-feeding forms such as *Essoidia epiceron*. There were various types of reptant forms which were carnivores or scavengers, of which there are two distinct lines: the pygocephalomorphs, which bear close resemblances to various modern forms; and the belotelsonids, which are unique unto themselves. And there are various quasi-natant-reptant types which may have been detritus or filter feeders, such as the genera *Crangopsis*, *Anthracophausia*, or *Peachella*. Where the poorly known Devonian and early Mississippian forms (*Eocaris*, *Devonocaris*, and *Palaeopalaemon*) fit is not recognized at this time.

The Late Paleozoic radiation is separate and distinct from the later Mesozoic-Cenozoic one. This fact remains clear. We may rightly debate at this time where to place the Late Paleozoic species within our present taxonomic scheme. We may retain them in a separate superorder Eocarida or choose to interpret them as an early, previously unsuspected radiation of the mysidacean-euphausiacean lines, but in either case they still remain separate and distinct from the later faunas.

It is interesting to note that this latter alternative returns again to the old ideas of B. N. Peach, i.e., of these creatures being "schizopods." Such a schizopodus theory has advantages in that it explains where the peracarids were in the Late Paleozoic. Traditional placement of Late Paleozoic forms within the "decapods" has always made it difficult to explain the sudden appearance of such advanced peracarids as isopods in the Late Permian and Mesozoic. The peracarids are now seen to have been present in the Paleozoic as a markedly divergent stock which bears little resemblance to the current largely "carapaceless" forms. This arrangement draws together again in the mysidaceans, the most primitive peracarids, and the euphausiaceans, the most primitive eucarids, as "schizopods," which now can begin to take on the aspects of an early radiation of caridoid types, forms imperfect in comparison to their Mesozoic-Cenozoic cousins. This may explain why the hoplocarids achieved such spectacular results in the Late Paleozoic, i.e., they were competing with caridoid forms which were capable of much improvement. The one form the hoplocarids began to perfect very early, i.e., the active carnivore of the paleostomatopods and stomatopods, has been the only hoploid form that has been able to successfully compete with the caridoid low-level carnivore forms. This early schizopodous radiation already indicates the directions in which later caridoid successes would come: in the Eucarida with the development and perfection of maxillepeds for effective food processing and laterally directed thoracopods for a reptant habit; in Peracarida with the perfection of habits for brooding the young and micro-division of available food resources.

SUMMARY

The Middle Pennsylvanian Essex Fauna Eocarida are examined. Some new species are described and the previously known forms re-examined. The marked similarities of these Late Paleozoic forms to elements of the modern fauna are documented. The Late Paleozoic caridoids are seen to be separate and distinct from later radiations but prefigure the adaptive types that are exploited in Mesozoic and Cenozoic Eucarida and Peracarida. The coherent nature of schizopodous caridoids seems to be verified.

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